

The shelled pteropods of the northeast Pacific Ocean (Mollusca: Heterobranchia, Pteropoda)

ARIE W. JANSSEN^{1*}, STEPHANIE L. BUSH² & NINA BEDNARŠEK³

¹Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands. E-mail: ariewjanssen@gmail.com.

²Smithsonian Institution National Museum of Natural History, Department of Invertebrate Zoology, 10th St & Constitution Ave NW, Washington, DC, USA, 20560. E-mail: bushsl@si.edu

³Southern California Coastal Water Research Project, 3535 Harbor Blvd #110, Costa Mesa, CA, USA, 926262. E-mail: ninab@sccwrp.org

*corresponding author.

Abstract

An overview of shelled pteropod species of the northeast Pacific Ocean, roughly north of 25°N and east of 160°W is presented. For the 34 recognised species (Limacinidae 6, Creseidae 4, Creseidae ? 2, Cuvierinidae 3, Cliidae 6, Cavoliniidae 10, Peraclidae 2, Clionidae 1) a brief description is given enabling identification. Data are based on several museum collections and the existing literature. For all species the original description and most important synonyms are referenced. Locations of type specimens are recorded as far as is known. All species are illustrated, for many species images of living specimens are included. *Cavolinia labiata* (d'Orbigny, 1835) is designated type species of *Orbignya* Adams, 1859.

Key words: Euthecosomata, Pseudothecosomata, taxonomy, systematics, Limacinoidea, Cavolinioidea, Cymbulioidea, Gymnosomata

This paper is dedicated to the memory of James H. McLean

Introduction

Pteropods are heterobranch gastropods that have evolved a holoplanktic way of life. Rare during the Late Cretaceous, pteropods evolved rapidly during the early and middle Cenozoic (Janssen & Peijnenburg 2017). They occur in all ocean basins and most seas worldwide, where they predominantly inhabit the epipelagic, though a number of species occur in meso- and bathypelagic waters. Pteropod distributions follow climatic zones, with generally high species diversity but low abundance in warm waters, and low diversity with high abundance in cold-water areas. They form an important part of the ocean food chain especially in polar ecosystems. For example, they can comprise a significant portion of the diet for early life stages of some commercially important fishes (Russell 1960). There is substantial literature on their morphology, anatomy, systematics, and distribution, much of which was summarised by Lalli & Gilmer (1989). While they regularly appear in plankton tows, pteropods rarely wash ashore or are found in sediment samples taken in areas where upwelling water is undersaturated with aragonite (Ω_{ar} : Feely *et al.* 2008). Such water promotes rapid dissolution of the pteropods' thin-walled, aragonitic shells.

Currently, shelled (euthecosome) pteropods are the topic of research on ocean acidification (OA) because of their extreme sensitivity to low Ω_{ar} (Bednaršek *et al.* 2014 and references therein). Upon exposure to corrosive water, their thin aragonitic shell starts to dissolve, leading to physiological impairments, and ultimately death (Bednaršek *et al.* 2014, 2017a, b). They have become OA indicators used to project the future state of ecological integrity (Bednaršek *et al.* 2017a and references therein). In comparison, nothing is known

about the OA effects on the adult stages of shell-less Pseudothecosomata and Gymnosomata, despite the fact that their most sensitive early-developmental stages have shells.

OA assessment of species' vulnerability or resilience across different pteropod groups requires an accurate systematic and taxonomic framework to allow for correct identification of investigated species. Current taxonomic work also paves the way for establishing linkages with molecular identification tools (barcoding, eDNA, etc.) needed for rapid monitoring and assessment of climate change effects on pteropods in the future.

The present interest in the Pteropoda as indicators of OA has stimulated renewed attention to their phylogenetic relationships. While molecular analyses have changed previous taxonomic evaluations by revealing unexpected biodiversity, available molecular information in most pteropod taxa is limited to the COI locus. Currently, family-level systematics are being investigated by integrative studies, including morphology and DNA sequencing (Burridge *et al.* 2017 and references therein).

Despite improved pteropod systematics summarized in Bouchet *et al.* (2017), there is still a lack of integration between taxonomic and molecular approaches for more accurate species identification, a baseline for OA vulnerability assessment can be conducted.

Particularity in the regions with high pteropod biodiversity, such as the northeast Pacific, a comprehensive synthesis of euthecosome taxonomic identification is still lacking. This is largely because there were no consistent sampling efforts focusing on pteropod community over large spatial scales across the North Pacific, as well as inconsistent net deployments that can easily miss pteropods in the water column. For this reason, an accurate and up-to-date synthesis of euthecosome pteropod taxa of the North Pacific is essential. In addition, taxonomic identifications are also assisted by the photographs to ensure accurate species identification.

In this work a summary and brief description of all shelled pteropods known from the northeast Pacific Ocean, roughly north of 25°N and east of 160°W, is presented. References for first descriptions are provided as are relevant synonyms and type localities.

Material and methods

Data for this paper are based on the collections housed in the Natural History Museum of Los Angeles County, Los Angeles, USA, the Santa Barbara Museum of Natural History, Santa Barbara, USA, the Naturalis Biodiversity Center, Leiden, The Netherlands, and the Smithsonian Institution National Museum of Natural History, Washington, DC, USA, as well as on specimens or data received from various researchers. Other data were compiled from the existing literature.

Illustrations are based on specimens in the collections mentioned above, other museum collections' specimens, or copied (with permission) from internet sources. Specimens from the northeastern Pacific were not available for all species, but illustrations of specimens from other areas are only included if their identification is certain.

Abbreviations

LACM	Natural History Museum of Los Angeles County, USA.
MCZR	Museo Civico di Zoologia, Roma, Italy.
MNHN	Muséum national d'Histoire Naturelle, Paris, France.
NHMD	Natural History Museum of Denmark, Copenhagen, Denmark.
NHMUK	The Natural History Musdeum, London, United Kingdom.
NMNZ	Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand.
NMR	Natuurhistorisch Museum, Rotterdam, The Netherlands.
RGM	Rijksmuseum van Geologie en Mineralogie, currently in Naturalis Biodiversity Center, Marine Biology (fossil Mollusca), Leiden, The Netherlands.
RMNH	Rijksmuseum van Natuurlijke Historie, currently in Naturalis Biodiversity Center, Marine Biology (recent Mollusca), Leiden, The Netherlands.
SBNMH	Santa Barbara Museum of Natural History, Santa Barbara, USA.
USNM	United States National Museum, Smithsonian Institution,Washington (DC), USA.

ZMA	Zoölogisch Museum, Amsterdam, The Netherlands, currently in RMNH.
ZMH	Zoologisches Museum, Hamburg, Germany.
ZMS	Zoological Museum, Stockholm, Sweden.

Systematics

Order Pteropoda Cuvier, 1804

Ptéropodes Cuvier, 1804: 232.

Description. Shelled or, in the adult stage, shell-less holoplanktic heterobranch gastropods have a modified foot that is a pair of parapodia ('wings') used for locomotion. For additional information on their habitat, soft part anatomy, etc. see Lalli & Gilmer (1989) and references therein.

Remarks. For a long time the name 'Pteropoda' has been used as an unofficial name for the orders Thecosomata and Gymnosomata. The molecular work of Klussmann-Kolb & Dinapoli (2006) revealed a close relationship between these two groups, which led to the re-establishment of the order Pteropoda as a sistergroup of the order Anaspidea P. Fischer, 1883 (= Aplysiida Pelseneer, 1906 emend. Bouchet *et al.* 2017).

Suborder Euthecosomata Meisenheimer, 1905

Thecosomata de Blainville, 1824: 271 (pars).
Euthecosomata Meisenheimer, 1905: 4.

Description. Pteropods with fragile (thin-walled) aragonitic shells in the adult stage, sinistrally coiled or bilaterally symmetrical. Epi- to bathypelagic, with diel vertical migration.

Limacinoidea Gray, 1840

Limacinidae Gray, 1840: 155 (Principle of Coordination).

Description. Shell of higher or lower conical or planorboid spiral, seemingly sinistral, but anatomically ultra-dextral. Protoconch not clearly separated from teleoconch. Columella straight (rarely twisted), not ending in rostrum, umbilicus present but almost completely closed in some species. Apertural margin simple or reinforced. Periostracum insignificant. Operculum present but frequently lost in adults.

Limacinidae Gray, 1840

Limacinidae Gray, 1840: 155.
Spirialidae Chenu, 1859: 113.
Spiratellidae Dall, 1921: 58.

Description. As for superfamily. Epi- to mesopelagic, rarely bathypelagic.

Heliconoides d'Orbigny, 1836

Heliconoides d'Orbigny, 1836: 159, 174. Type species (SD Herrmannsen 1846: 514) *Atlanta inflata* d'Orbigny, 1835 = *Heliconoides inflatus* (d'Orbigny, 1835). Tropical and subtropical, worldwide.

Protomedea Costa, 1861: 73. Type species (SD Fischer 1883: 430) *Protomedea elata* Costa, 1861 = *Heliconoides inflatus* (d'Orbigny, 1835). Mediterranean.

Embolus Jeffreys, 1869: 114. Type species (OD) *Spirialis rostralis* Eydoux & Souleyet, 1840 = *Heliconoides inflatus* (d'Orbigny, 1835).

Skaptotion Curry, 1965: 368. Type species (M) *Skaptotion bartonense* Curry, 1965. Eocene, United Kingdom.

Description. Last whorl and apertural margin reinforced by subperipheral belt on internal wall, usually

projecting as a rostrum on the aperture margin because of damaged, extremely thin apertural margin above and below the belt.

Remarks. Genus monotypic with a single Recent species, but many fossil species. Possibly polyphyletic because the phylogenetic lineage of numerous extinct species is difficult to determine. Cretaceous (Campanian) to Recent (Janssen & Goedert 2016).

Heliconoides inflatus (d'Orbigny, 1835)

(Figure 1a–c)

A[llanta] [sic] inflata d'Orbigny, 1835: pl. 12, figs 16–19.

Atlanta inflata d'Orbigny, 1836: 174. About 82 syntypes in poor condition (NHMUK 1854.12.4.38: van der Spoel 1976: 188). Atlantic and Indo-Pacific oceans, 36°N–36°S.

Spirialis rostralis Eydoux & Souleyet, 1840: 236. No types available. No type locality mentioned.

Limacina scaphoidea Gould, 1852: 485; atlas (1856) figs 602–602a. Types never indicated (van der Spoel 1976: 188). Equatorial Atlantic.

Protomedea elata O.G. Costa, 1861: 74, pl. 11, fig. 5a–c. No types available. Mediterranean.

Description. Very fragile, planorboid shell, 1.5× wider than high, flattened to slightly sunken apical plane. Shell height to 1.6 mm. Initial whorl occasionally slightly raised. Three convex whorls, last one inflated, base perfectly rounded, umbilicus present, 1/6 of shell diameter. Aperture wide, as high as entire shell. Last whorl, apertural margin internally reinforced by narrow internal, subperipheral belt. Operculum present, transparent.

Distribution. Tropical to subtropical. In northeast Pacific to about 40°N. Epipelagic. Abundant, but more rare to the North.

Remarks. Two forms can be distinguished (Janssen 2004: 109) with a subperipheral belt starting on earlier whorls, continuing to apertural margin, or a subperipheral belt only present in second half of last adult whorl and whorl from there on more or less swollen. It is unknown if these two morphological forms represent two taxa, as transitional forms also occur. It is possible that the forms have different geographical distributions.

Genus *Limacina* Bosc, 1817

Limacina Bosc, 1817: 42. Type species (OD) *Clio helicina* Phipps, 1774. Northern (subarctic) area of Atlantic and Pacific oceans.

Spiratella de Blainville, 1817: 407. Type species (OD) *Clio helicina* Phipps, 1774. Northern (subarctic) area of Atlantic and Pacific oceans.

Heterofusus Fleming, 1823: 498, pl. 15, fig. 2. Type species (SD Gray 1847) *Fusus retroversus* Fleming, 1823. Northern Atlantic Ocean.

Spirialis Eydoux & Souleyet, 1840: 235. Type species (SD Herrmannsen 1847: 489) *Atlanta trochiformis* d'Orbigny, 1835. Tropical and subtropical regions worldwide.

Scaeia Philippi, 1844: 164. Type species *Trochus lunaris* Gmelin, 1791 (SD Herrmannsen 1847: 418, declared *nomen oblitum* by Janssen 2012a: 30) = *Limacina retroversa* Fleming, 1823: 498. Pleistocene central Mediterranean.

Crino Gistel, 1848: 166. Type species (OD) *Crino arctica* Fabricius, 1780 = *Limacina helicina* (Phipps, 1774). Northern (subarctic) area of Atlantic and Pacific oceans.

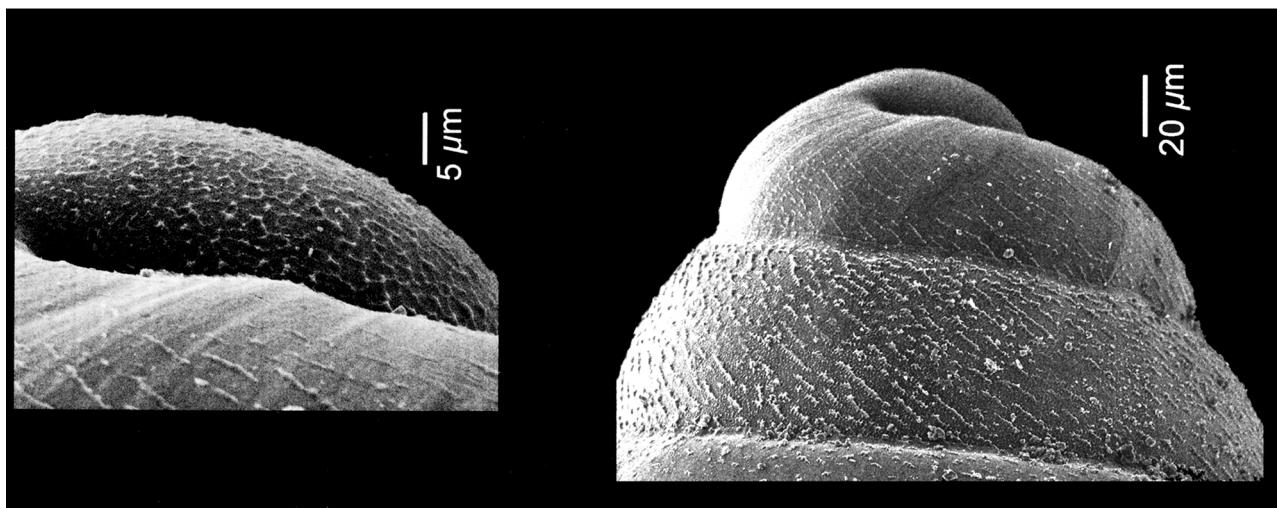
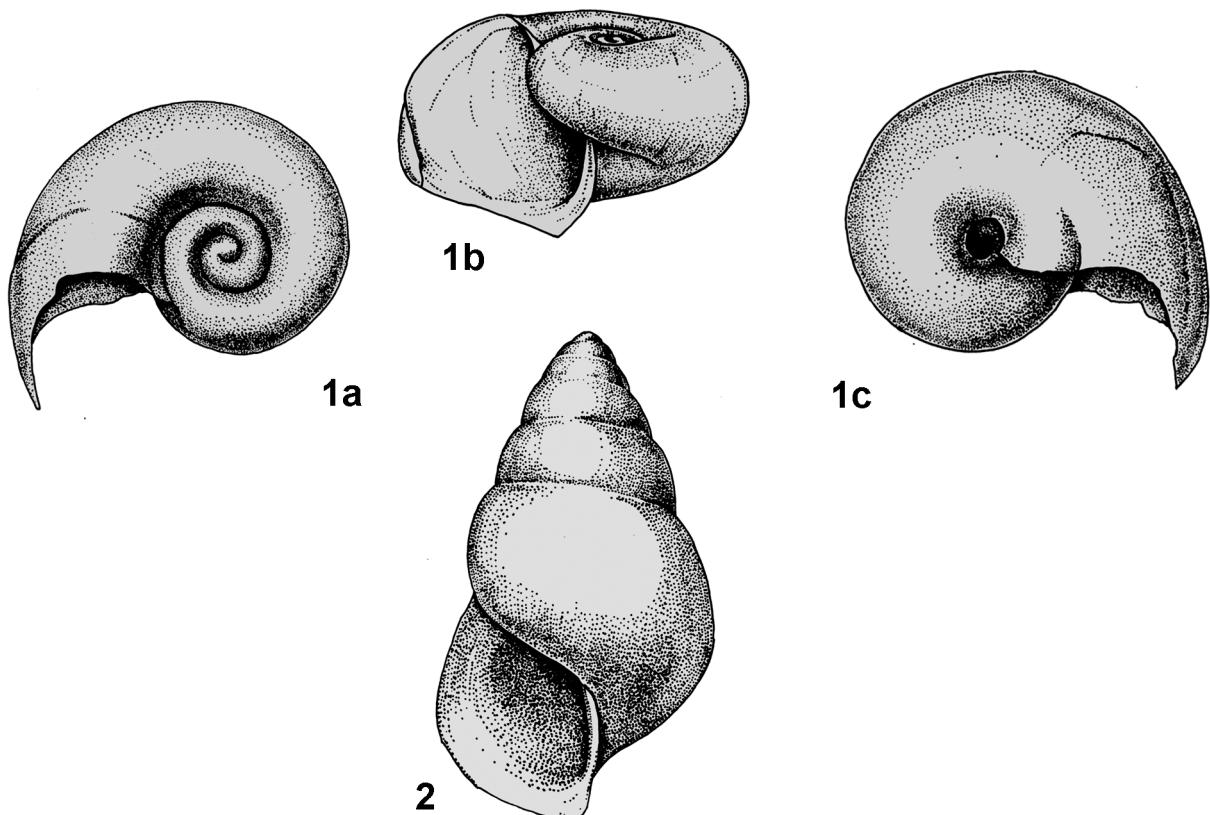
Valvatina Bornemann, 1855: 318. Type species (M) *Valvatina umbilicata* Bornemann, 1855. Oligocene, Germany.

Munthea van der Spoel, 1967: 37. Type species (SD Janssen 2003) *Munthea trochiformis* (d'Orbigny, 1835). Tropical and subtropical regions worldwide.

Pygmella Tembrock, 1989: 242. Type species (OD) *Spiratella (Pygmella) pygmaea* (Lamarck, 1805). Eocene, Paris Basin, France.

Description. Apical plane not flattened but in higher or lower spiral. Apertural margin simple.

Remarks. The genera *Limacina* Bosc, 1817 and *Spiratella* de Blainville, 1817 were both introduced in December 1817 and are based on the same type species. Over time the name *Limacina* was predominantly used by biologists, whereas paleontologists usually applied the name *Spiratella*. Janssen & Zorn (2001) concluded that priority should be given to *Limacina*.



3a

3b

FIGURES 1–3. *Heliconoides, Limacina*. **1a–c.** *Heliconoides inflatus* (d'Orbigny, 1835). California. Shell diameter 1.5 mm (from McGowan, 1968). Note thickening of apertural margin in middle figure, showing presence of internal belt. **2.** *Limacina bulimoides* (d'Orbigny, 1835), California. Shell height 3.0 mm (from McGowan 1968). **3a–b.** *Limacina bulimoides* (d'Orbigny, 1835), microornamentation on nucleus (left) and early whorls (right); specimen from the eastern Mediterranean, core T87/2/20G; RGM 569378b (from Janssen 2012a: fig. 46D–E).

***Limacina bulimoides* (d'Orbigny, 1835)**

(Figures 2, 3a–b)

A[llanta] [sic] bulimoides d'Orbigny, 1835: pl. 12, figs 36–38. *Atlanta bulimoides* d'Orbigny, 1836: 179. Syntypes listed by Gray (1854: 7) not traceable in NHMUK or MNHN (van der Spoel 1976: 188). 'Deux grands Océans' [Atlantic, Pacific] between 34°N and S (d'Orbigny 1836: 179).

Description. Shell high spired, to 3 mm high, ~1.5–1.7× higher than wide; up to six moderately convex whorls separated by incised suture. Aperture higher than wide, pointed below, above. Apertural margin simple. Umbilicus very small to almost absent. Surface of shell with faint growth lines, very fine microgranulations, especially on nucleus, first whorls. Fresh specimens with brownish color along suture and at aperture.

Distribution. Tropical to subtropical, in the northeast Pacific south of 40°N, epipelagic, uncommon.

***Limacina helicina helicina* (Phipps, 1774)**

(Figures 4, 5a–b)

Clio helicina Phipps, 1774: 195. No types available. Subarctic seas.

Argonauta arctica Fabricius, 1780: 386. No types available. Northern Atlantic Ocean.

Limacina helicinalis Lamarck, 1819: 291. No types available. 'Les mers du nord' (northern seas).

Spiratella planospira Rehder, 1942: 108, pl. 23, figs 5–7. Holotype USNM 535416. Type locality North Atlantic Ocean, 49°36'N, 28°54'W.

Description. Shell of brownish color when fresh, wider than high to almost as wide as high, with up to six whorls in low conical spire, separated by distinct suture. Last whorl large, swollen. Shell surface from 4th whorl onward with regular ornament of fine radial riblets. Aperture large, with straight columellar side, rounded outer lip. Umbilicus present, 1/6–1/4 shell diameter. Operculum present. Shell height to about 6 mm, H/W-ratio 0.70–1.10.

Distribution. Epipelagic species (to ~300 m). North Atlantic and North Pacific oceans, in the Pacific Ocean roughly between 45 and 65°N, more to the south, to c. 30°N in the eastern part of the North Pacific. Predominantly between 40 and 60°, with the greatest abundances in the northern part of that area (McGowan 1963: as *L. helicina* A). This species has been collected from under polar ice and may occur locally in large populations.

Remarks. A form with a somewhat elevated spire (H/W-ratio c. 0.9 to over 1.1 (McGowan 1963: fig. 2 left), described as f. *acuta* van der Spoel (1967: 40, fig. 5e; unavailable name: infrasubspecific), co-occurs with the typical form.

Juvenile specimens of *Limacina helicina helicina* less than four whorls do not have radial ornament and cannot be distinguished from *L. helicina pacifica*. Molecular analyses (Bednářek unpubl. data) do not differentiate between these two taxa, thus herein they are interpreted as subspecies on the basis of different distributions, as indicated by McGowan (1963).

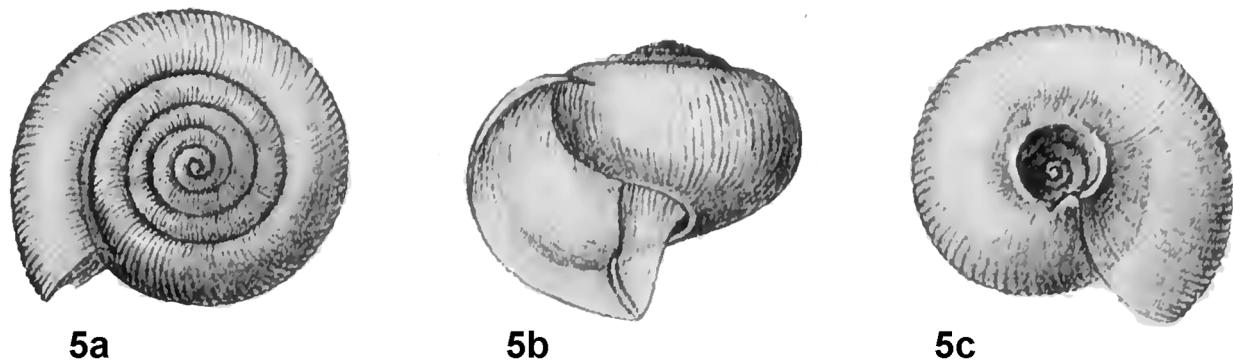
Two forms or subspecies, *Limacina helicina* (f.) *antarctica* Woodward, 1854 and *L. helicina* (f.) *rangi* d'Orbigny, 1835, are recorded from the Antarctic region. Hunt *et al.* (2010), however, restricted the species *L. helicina* on the basis of molecular work to the northern oceans, which makes *L. rangi* the valid name for the southern seas. Two subspecies are found in the northeast Pacific (McGowan 1963).

***Limacina helicina pacifica* Dall, 1871**

(Figures 6, 7a–c)

Limacina pacifica Dall, 1871: 138. Lectotype (van der Spoel 1976: 187, fig. 30) USNM 56767. Monterey (restricted by van der Spoel 1976).

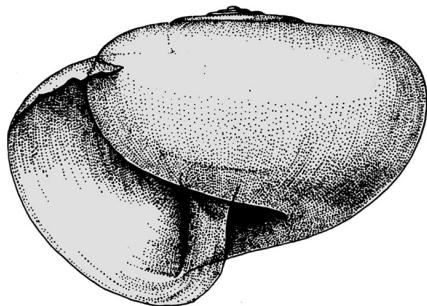
Description. Subspecies *L. helicina pacifica* differs by the absence of radial ornament. Shell surface with faint growth lines only; spire relatively low conical (e.g. H 2.99, W 4.14 mm).



FIGURES 4–5. *Limacina*. 4. *Limacina helicina helicina* (Phipps, 1774). Sea of Japan, photographed during SCUBA-diving; shell diameter estimated ~6 mm (courtesy of Alexander Semenov). 5. *Limacina helicina helicina* (Phipps, 1774); shell width 4 mm. Jan Mayen, North Atlantic Ocean (from Sars, 1878).

Remarks. According to McGowan (1963) and van der Spoel (1967: fig. 336) the subspecies is found in the northern Pacific Ocean, predominantly between 30 and 60°N, present from the Bering Sea to the Gulf of California (Angulo-Campillo *et al.* 2011). Both subspecies also occur in the estuarine regime of the Salish Sea. *Limacina helicina* is the best studied and characterized pteropod species used in OA research (Bednaršek *et al.* 2017).

A related subspecies was described from the Sea of Okhotsk, west of Kamchatka and the Kurilian Islands, as *Limacina helicina ochotensis* Shkoldina (1999: 331, figs 2–5). In this subspecies the spire is depressed as in the typical form of *L. helicina helicina*, with the same radial ornament, but the last whorl is comparatively large and the shell is almost as high as it is wide.



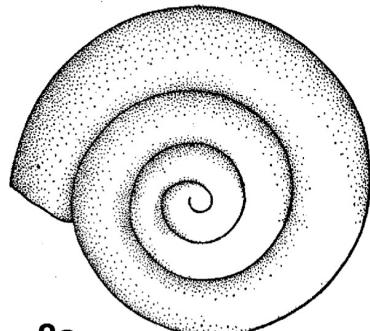
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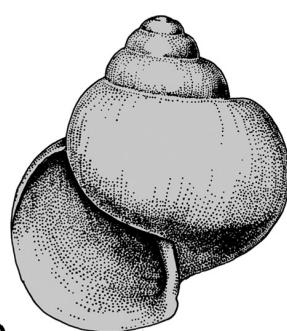
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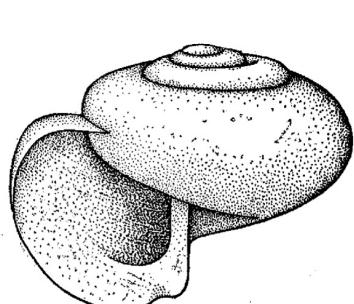
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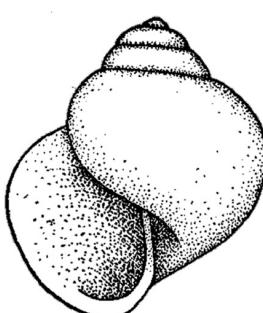
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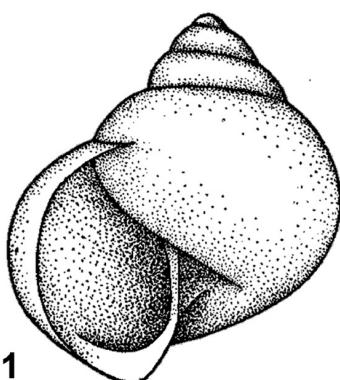
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FIGURES 6–11. *Limacina*. **6.** *Limacina helicina pacifica* Dall, 1871. California. Shell diameter 2.0 mm (from McGowan 1968). **7.** *Limacina helicina pacifica* Dall, 1871. Meyers Point, Cleveland Peninsula, Outer Ketchikan County, Alaska, 55.750°N, 132.260°W, depth 0 m; SBMNH 10247. Shell diameter 4.4 mm. Photo by Ronald Pouwer. **8.** *Limacina lesueurii* (d'Orbigny, 1836). Shell height 0.84 mm; North Pacific Ocean, 14°N 149°W (from Tokioka 1955). **9.** *Limacina trochiformis* (d'Orbigny, 1835), diameter 0.95 mm. California (from McGowan 1968). **10, 11.** *Limacina trochiformis* (d'Orbigny, 1835), shell height 0.67 mm (10) and 0.87 mm (11). Pacific Ocean (from Tokioka, 1955).

***Limacina lesueurii* (d'Orbigny, 1836)**

(Figure 8a–b)

Atlanta Lesueurii d'Orbigny, 1836: 177, pl. 20, figs 12–15. Five syntypes in bad condition NHMUK 1854.12.4.38 cat. Nr 64 (van der Spoel 1976: 188). Atlantic and Pacific oceans.

Description. Shell wider than high, low conical spiral of ~4–5 rather convex whorls. Last whorl large, occupying more than 3/4 of total shell height. Base regularly rounded, with one or two incised spirals around very narrow umbilicus. Aperture large, obliquely elliptical, with straight columellar part and regularly rounded, simple margin. Maximum diameter ~1.5 mm.

Distribution. Bisubtropical in all oceans. In the northeast Pacific to ~40°N. Epipelagic. Uncommon, especially to the North.

Remarks. Morphologically similar to juveniles of *Limacina helicina* sensu lato. That species, however, has no spirals on its base, has a wider umbilicus, reaches far larger dimensions, and has a more northern distribution.

***Limacina trochiformis* (d'Orbigny, 1835)**

(Figures 9–11)

A[llanta] [sic] trochiformis d'Orbigny, 1835: pl. 12, figs 29–31.

Atlanta trochiformis d'Orbigny, 1836: 177. Syntypes? (Gray 1854: 7, van der Spoel 1976: 188). Pacific Ocean 20–30°S and 89–92°W (of Paris); in the Atlantic Ocean 28°S–34°N.

Limacina contorta Sykes, 1905: 327, 1 fig. Types are not in National Museum of Wales, Cardiff (H. Wood pers. comm. 8/2017), they might be in NHMUK. Mediterranean.

Description. Shell very small, height to ~1 mm, with conical spire, slightly higher than wide, apical angle slightly less than 90°, about five rather convex whorls, separated by incised suture. Aperture occupying half shell height or slightly more, with somewhat concave columellar side, regularly curved margin. Umbilicus very small. Shell transparent, sometimes brownish in color on thickest parts. Shell smaller and less conical and with deeper suture than in *L. bulimoides*.

Distribution. Tropical/subtropical epipelagic. In northeast Pacific mainly south of 30–33°N (McGowan 1960, Angulo-Campillo *et al.* 2011, Bednaršek unpublished). Uncommon, more common to the south.

Cavolinioidea Gray, 1850 (1815)

Hyalinea Rafinesque, 1815: 140 [ICZN Art 40(2)].

Cavolinidae Gray, 1850: 3 (emended Fischer, 1883: 434, Principle of Coordination).

Description. Shell conical or bilaterally symmetrical. Protoconch usually clearly separated. Operculum absent.

Remarks. Molecular work of Burridge *et al.* (2017) has acknowledged the monophyly of uncoiled Euthecosomata, validating the superfamily Cavolinioidea. The currently applied subdivision in families (Janssen 2003, Bouchet & Rocroi 2005) based on shell-morphological characteristics, however, was not supported. Burridge *et al.* (2017: 13) found only one supported subdivision within Cavolinioidea based on maximum likelihood-produced phylogenies, with *Creseis* as a monophyletic group and a sister clade to *Cavolinia*, *Clio*, *Cuvierina*, *Diacavolinia*, *Diacria*, *Hyalocylis* and *Styliola*. This led Bouchet *et al.* (2017) to recognise just two families, Cavoliniidae and Creseidae within the Recent superfamily Cavolinioidea, considering Cuvierinidae and Cliidae synonyms of Cavoliniidae.

However, the general morphology of species previously included in Cuvierinidae and Cliidae is so analogous and so strongly different from more typical Cavoliniidae that further detailed, integrative research is expected to result in a more robust subdivision validating these families.

For the genera *Hyalocylis* and *Styliola* one or even two new families may be desirable (compare Corse *et al.* 2013: fig. 2; Burridge *et al.* 2017: fig. 2) and it is expected that ongoing molecular work will shed more light on this. In anticipation, these genera are here still included in Creseidae as has been customary so far (but with a query).

Creseidae Rampal, 1973

Creseiidae [sic] Rampal, 1973: 1347.

Description. Shell elongated, conical, straight or curved; dorsal and ventral parts not separated by lateral carinae, transverse section circular or elliptical, lacking lateral slits. Shell surface only with growth lines or transverse annulation. Epi- to mesopelagic.

Remarks. Creseidae seems to be polyphyletic (Klussmann-Kolb & Dinapoli 2006, Corse *et al.* 2013, Burridge *et al.* 2017). Current (Corse *et al.* 2013: fig. 2, Burridge *et al.* 2017: fig. 2) molecular work indicates that the genera *Styliola* and *Hyalocylis* take a separate position, apart from Creseidae. The complicated history of *Creseis* nomenclature was discussed in Gasca & Janssen (2014) and Janssen (2018).

Genus *Creseis* Rang, 1828

Cleodora (Creseis) Rang, 1828: 305. Type species (SD Fischer 1883) *Cleodora acicula* Rang, 1828. Tropics and subtropics worldwide.

Creseis (Boasia) Dall, 1889: 80. Type species (M) *Creseis (Boasia) chierchiae* Boas, 1886.

Description. Shell elongated, conical, transverse section circular, surface smooth or with transverse annulation, apical angle variable 3–15°. Shell height of adult specimens <2 to >30 mm.

Remarks. The names *Cresis*, *Crisia* and *Criseis*, sometimes found in older literature, are erroneous spellings of *Creseis*.

***Creseis acicula* (Rang, 1828)**

(Figures 12–13)

Cleodora (Creseis) clava Rang, 1828: 317, pl. 17, fig. 5. Lectotype MNHN-IM-2000-33844 (van der Spoel 1976: 189, Janssen 2007: fig. 7b). Banc des Aiguilles, South Africa.

Cleodora (Creseis) acicula Rang, 1828: 318, pl. 17, fig. 6. Lectotype MNHN-IM-2000-33842 (van der Spoel 1976: 189, Janssen 2007: fig. 7a). Indian Ocean.

Creseis acus Eschscholtz, 1829: 17, pl. 15, fig. 2. Type material unknown. Coast of Brazil.

Styliola recta Gray, 1850: 18. Syntypes should be in NHMUK. Sicily.

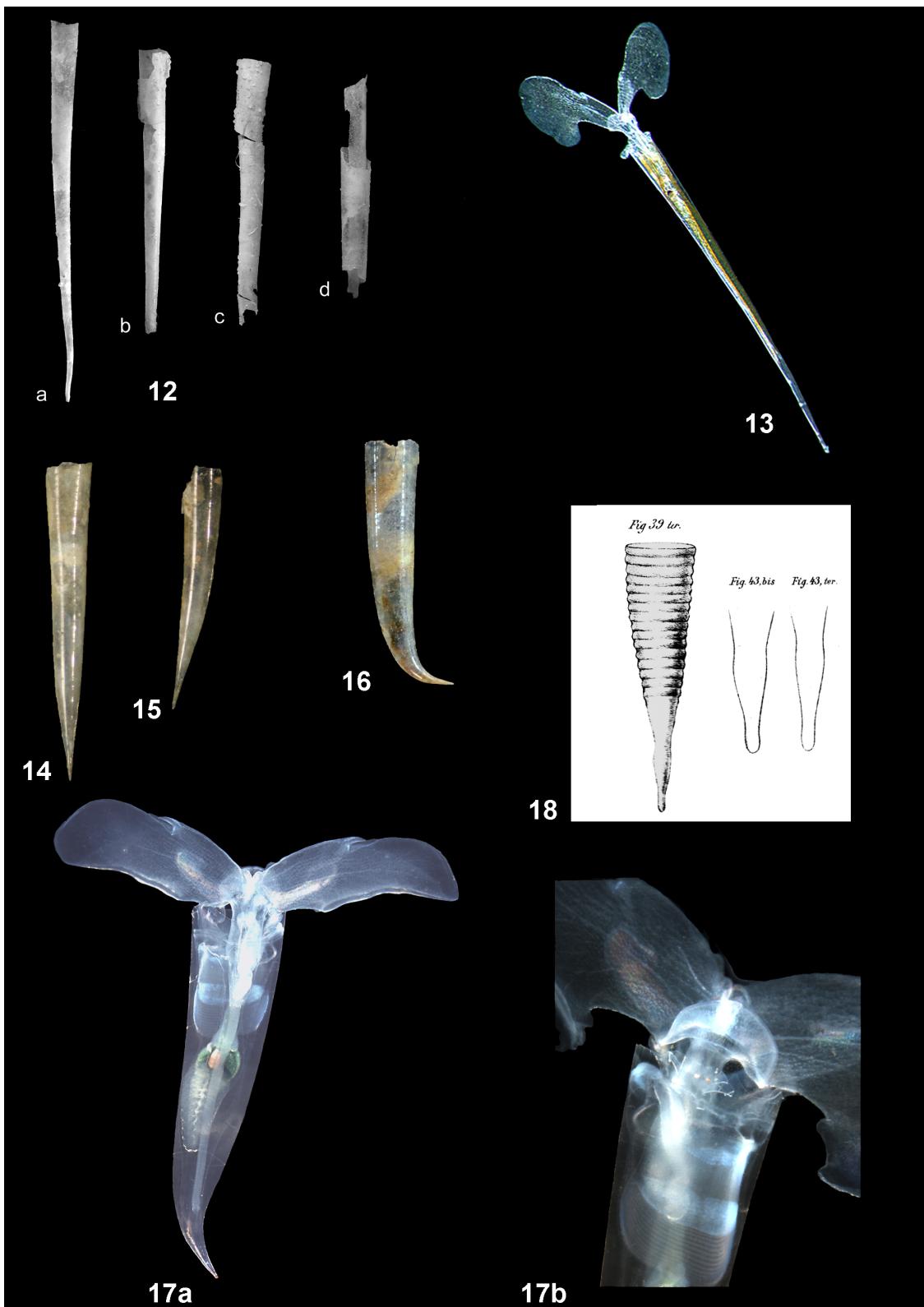
Cresis spiniformis Benoit, 1843: 6. No types available. San Rainiero, Sicily.

Dentalium ecostatum Kirk, 1880: 806. Holotype NMNZ M.000262. Type locality ‘Waikanae’ (error = mislocalised foreign: <https://collections.tepapa.govt.nz/object/153267>).

Description. Shell very elongately conical, needle-shaped, apical angle ~3°, straight or slightly irregular, with circular transverse section. Shell height to >30 mm, width to ~1.4 mm. Protoconch not clearly separated, with rounded tip.

Distribution. In northeast Pacific mainly south of 35°N, but occasionally up to 48°N (Abbott 1954: 294, Rampal 2002). Common.

Remarks. The distinction of *Creseis* species for a long time has been difficult and subject to many discussions and speculations, because of a rather ambiguous first description (Frontier 1965, Rampal 1985, 2002, 2017, Janssen 2007, 2012a, Gasca & Janssen 2014). Especially the interpretations of *Creseis acicula* (Rang, 1828) and *C. clava* (Rang, 1828) have been confusing for a long time, and only clarified when illustrations of the lectotypes of both became available, acknowledging the synonymy of these names. The choice of *C. clava* as the valid name for the type species of *Creseis* instead of *C. acicula*, as done by Janssen (2007) and Gasca & Janssen (2014), cannot be substantiated: d’Orbigny (1836: 123), acting as First Reviser (ICZN 1999: Art. 24.2.1) had already established the name *C. acicula* (although misspelled as *aciculata*) as valid (Janssen, 2018).



FIGURES 12–18. *Creseis*. 12a–d. Lectotypes of *Creseis acicula* (Rang, 1828) (a, shell height 12.5 mm). Lectotype (b) and paralectotypes (c–d) of *C. clava* (Rang, 1828). Photographs by courtesy of Pierre Lozouet (MNHN). From Janssen (2007). 13. *Creseis acicula* (Rang, 1828), locality and size not mentioned (courtesy of Russell R. Hopcroft). 14, 15. *Creseis conica* Eschscholtz, 1829, straight and slightly curved forms; height of left specimen 7.5 mm. Bay of Bengal, Indian Ocean. NMR 47663. 16. *Creseis virgula* (Rang, 1828), shell height 8 mm. Indian Ocean. NMR 47665. 17a–b. *Creseis virgula* (Rang, 1828). Gulf of California. Shell height 7.2 mm. Photos by Stephanie L. Bush. 18. *Creseis chierchiai* Boas, 1886; complete shell and two protoconchs magnified; shell height 2.5 mm. Panama (from Boas 1886).

***Creseis chierchiae* (Boas, 1886)**

(Figure 18)

Cleodora chierchiae Boas, 1886: 62, 202, figs 39ter, 43bis-ter. About 60 probable syntypes, partly decalcified, NHMD-91145.

Panama, 110°E, 10°N.

Creseis virgula constricta Chen & Bé, 1964: 194, figs 3d, 4d. Holotype ?. Surface water 44°N, 41°W.

Creseis bulgia Sakhtivel, 1974: 619, figs 1–2. Holotype Biological Centre, Cochin 10 BC-0239-06-36, Indian Ocean, off Kalpeni Island, Laccadives Sea, 10°04'N, 73°36'E.

Description. Shell very small (height 2.5 mm), conical, straight or very slightly curved, especially in lower part, apical angle ~15°, transverse section circular. Larval shell 0.42–0.58 mm high, with rounded tip, initial part tubiform, followed by swelling, separated from teleoconch by clear, gradual constriction. Surface of adult shell, or only part of it, transversely annulated in typical form, smooth, apart from vague growth lines in some (= *C. virgula constricta* Chen & Bé, 1964, currently considered a forma of *C. chierchiae*, see Janssen, 2007: 65).

Distribution. In the northeast Pacific recorded from 36°04.0'N, 162°13.5'E (McGowan 1960: 161). Patchy distribution, Uncommon.

Remarks. The species has a complicated history (van der Spoel 1967, Richter 1976, Gasca & Janssen 2014).

***Creseis conica* Eschscholtz, 1829**

(Figures 14–15)

Creseis conica Eschscholtz, 1829: 17, fig. 3. Syntypes ? Coast of Brazil.

Creseis conica A. Costa, 1869: 45, pl. 1, fig. 2).

Cleodora conoidea A. Costa, 1873: 17, pl. 4, fig. 6. Nom. nov. for *Creseis conica* A. Costa, 1869 non Eschscholtz, 1829.

Styliola vitrea Verrill, 1872: 211, pl. 6, fig. 7. Syntypes should be in the Museum of Yale College. Off Gay Head, Martha's Vineyard.

Cleodora flexa Pfeffer, 1879: 241, figs 15–16. Syntypes possibly in Museum für Naturkunde, Berlin, Germany? Recorded from three localities in the Coral Sea, NE of Australia.

Creseis rotunda G.B. Sowerby II, 1878: pl. 5, fig. 28a–b. Syntypes in MNHUK? Type locality unknown.

Creseis conica falciformis Rampal, 2002: 233, figs 9P–T, 11. Holotype MNHN-IM-2000-33854 and paratypes MNHN-IM-2000-33855. Type locality 'Golfe de Guinée', 01°20'S, 05°48'E.

Description. Elongated conical shell, straight or slightly curved lengthwise, surface smooth, shell height to ~8 mm, width at aperture 1 mm. Apical angle > 3–11°.

Distribution. In northeast Pacific south of ~40°N. Epipelagic, abundant to the south. Common.

***Creseis virgula* (Rang, 1828)**

(Figures 16, 17a–b)

Cleodora (Creseis) virgula Rang, 1828: 316, pl. 17, fig. 2. Syntypes? Atlantic Ocean and Antilles.

Creseis unguis Eschscholtz, 1829: 17, pl. 15, fig. 4. No syntypes available. North Atlantic near Canary Islands.

Creseis cornucopiae Eschscholtz, 1829: 17, fig. 5. No syntypes available. In der Südsee, in der Nähe der niedern Inseln [Southern sea, near the lower islands].

Creseis caligula Eschscholtz, 1829: 18, pl. 15, fig. 6. No syntypes available. South Sea, near the Equator.

Hyalaea corniformis d'Orbigny, 1836: 120. No type specimens available. All warm seas N and S of the equator.

Cleodora munda Gould, 1852: 489, 1856: pl. 51, figs 607, 607a. Equatorial Atlantic.

Cleodora placida Gould, 1852: 490, 1856: pl. 51, fig. 606. Equatorial Atlantic.

Creseis virgulata Locard, 1886: 24 [incorrect spelling of *virgula*].

Styliola africana Bartsch, 1915: 3, pl. 34, fig. 4. Holotype USNM 249794. Port Alfred.

Creseis virgula frontieri Rampal, 2002: 234. Holotype MNHN-IM-2000-33857. Gulf of Guinea.

Description. Shell strongly curved dorsally in posterior part only, straight or slightly curved ventrally in anterior parts of larger specimens, apical angle 10°–15°, transverse section circular. Shell height to ~12 mm.

Distribution. In northeast Pacific to ~42°N. Common, less frequent to the north.

Creseidae Rampal, 1973?

Remark. The genera *Hyalocylis* and *Styliola* are currently included in Creseidae, but ongoing molecular work (see above) suggests that for these genera a separate family might be desirable. Awaiting further results we retain them in Creseidae, but with a query.

***Hyalocylis* Fol, 1875**

Hyalocylis Fol, 1875: 177. Type species (M) *Hyalocylis striata*. Tropics and subtropics.
Hyalocylis Fischer, 1883: 436 [unjustified emendation].

Description. Shell to 9 mm, conical, slightly curved in apical part, distinctly annulated, slightly oval in transverse section, aperture simple, protoconch usually absent, opening covered with tissue.

***Hyalocylis striata* (Rang, 1828)**

(Figures 19–20)

Cleodora (Creseis) striata Rang, 1828: 315, pl. 17, fig. 3. Eight syntypes (van der Spoel 1976: 189) MNHN-IM-2000-33846.
Atlantic and Indian Ocean.

Description. Same as for genus.

Distribution. In northeast Pacific, to ~40°N. Uncommon.

Remarks. Current molecular work (e.g. Burridge *et al.* 2017: fig. 2) indicates a more remote relationship with Creseidae than is currently accepted. The larval shell of this species remained unknown for a long time or was interpreted erroneously by presuming that *Creseis chierchiae* in fact represents its larval shell. Richter (1976), van der Spoel & Newman (1990) and Janssen (2012a: 37ff) clarified the morphology of that shell part. It is evident, however, that living specimens are usually found without a protoconch, the apical opening of the shell presumably closed with organic tissue.

***Styliola* Gray, 1847**

Styliola Gray, 1847: 203. Type species (M) *Styliola recta* Gray, 1850 = *Styliola subula* (Quoy & Gaimard, 1827). Tropical and subtropical seas worldwide

Description. Shell conical, straight or somewhat curved apically, transverse section circular, apart from groove running in weak spiral towards aperture, forming dorsal spine on apertural margin. Protoconch pointed, with weak inflation between two constrictions.

***Styliola subula* (Quoy & Gaimard, 1827)**

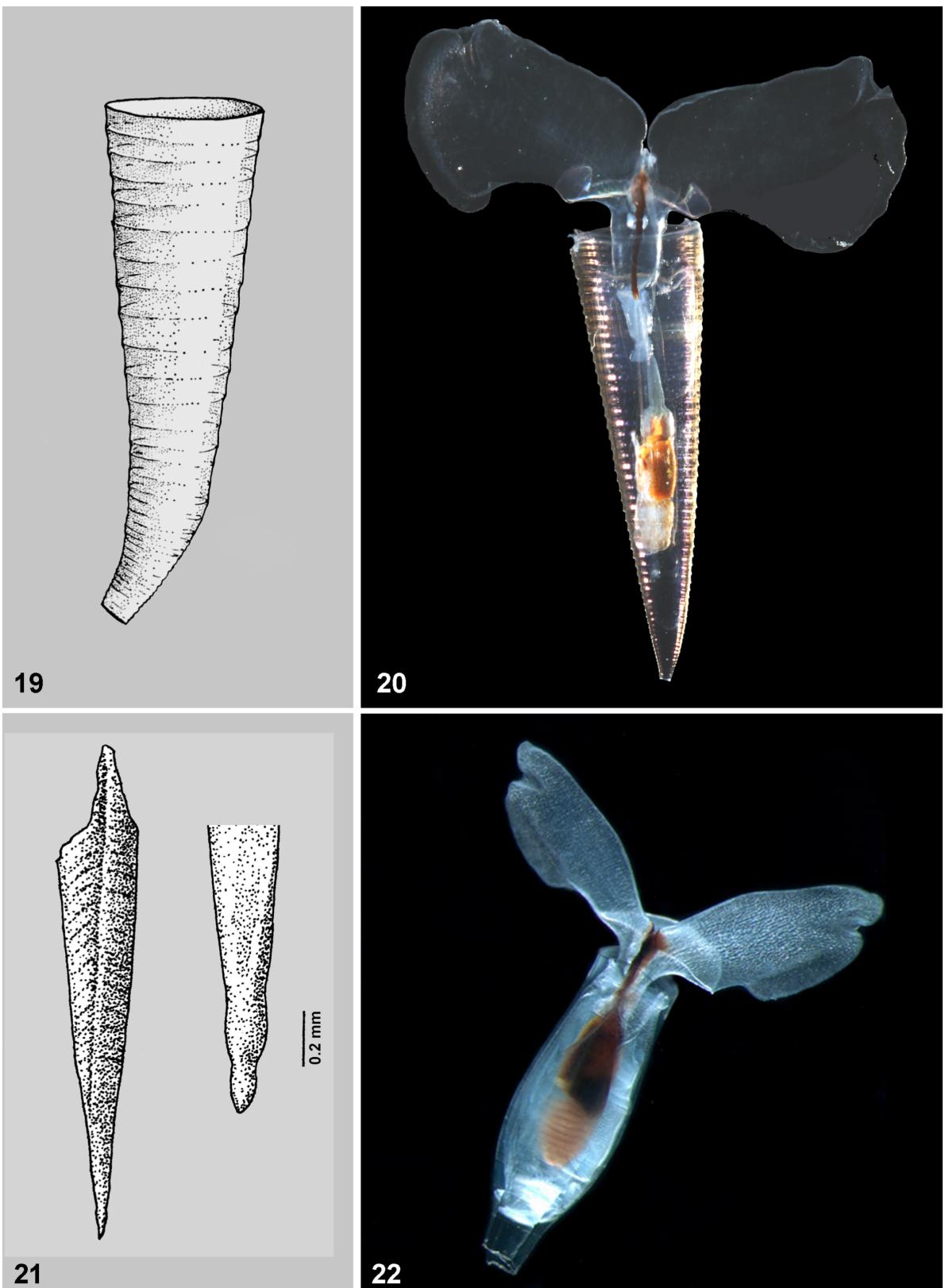
(Figure 21)

Cleodora subula Quoy & Gaimard, 1827: 233, pl. 8D, figs 1–3. Neotype RMNH 57267 (Janssen 1999: 19, fig. 3). South of Palma, Canary Islands.

Creseis spinifera Rang, 1828: 313, pl. 17, fig. 1. Syntypes not in MNHN; Ocean (Atlantic ?) between 30°N and 26°S; Indian Ocean; Antilles.

Description. Same as for genus.

Distribution. In northeast Pacific to ~40°N. Epipelagic. Uncommon.



FIGURES 19–22. *Hyalocylis*, *Styliola*, *Cuvierina*. **19.** *Hyalocylis striata* (Rang, 1828), shell height c. 8 mm. Southern Indian Ocean, 2°57'S 99°36'E (from van der Spoel 1967: fig. 46a). **20.** *Hyalocylis striata* (Rang, 1828), Gulf of California, Baja del Sur; shell height 8 mm. Photo by Stephanie L. Bush. **21.** *Styliola subula* (Quoy & Gaimard, 1827). Neotype, shell height 7.3 mm; RMNH 57267, Tydernan Selvagens-Canary Islands Expedition, 1980. CANAP IV, sta. 4.117; Canary Islands, S. of Palma, 28°26'N, 17°51'W, depth 503 m, gravel, sand, and shells; van Veen grab, 28-V-1980; a: dorsal view, b: protoconch (from Janssen, 1999). **22.** *Cuvierina columnella* (Rang, 1827), locality and size not given (courtesy of Russell R. Hopcroft).

Cuvierinidae van der Spoel, 1967 (1840)

Cuvieridae Gray, 1840: 148 [invalid because based on junior homonym *Cuvieria* Rang, 1827 (non Cuvier ex Peron, 1817, nec Lesueur & Petit, 1807, nec Leach, 1814, nec Jaeger 1833)].

Tripteridae Gray, 1850: 23 [declared *nomen oblitum* ICZN Art. 23.9 by Bouchet & Rocroi (2005: 175)].

Cuvierininae van der Spoel, 1967: 78. Raised to family level by Beu & Maxwell (1990: 424).

Description. Bottle shaped to almost cylindrical, somewhat flattened ventrally near aperture. Protoconch conical pointed with slight inflation, usually shed, opening closed by convex calcareous septum. Aperture reniform to rounded triangular. Shell surface smooth or with radial microornamentation.

Remarks. See note on the validity of this taxon under Cavolinioidea above.

***Cuvierina* Boas, 1886**

? *Triptera* Quoy & Gaimard, 1825: 76, pl. 2, fig. 5. Type species (M) *Triptera rosea* Quoy & Gaimard, 1825 (= ? *Cuvierina* sp. indet.). Type specimen lost. Port Jackson, Australia.

Cuvieria Rang, 1827: 322 (non Lesueur & Petit, 1807: pl. 30: Coelenterata). Type species (M) *Cuvieria columnella* Rang, 1827. Indian Ocean.

Tripter Rang, 1829: 116. Incorrect spelling of *Triptera*.

Tripteris Menke, 1830: 9. Unnecessary replacement name for *Triptera* Quoy & Gaimard, 1825.

Herse Gistel, 1848: 174 (replacement name for *Cuvieria* Rang, 1827. Homonym of *Herse* Oken, 1815: 762 (Lepidoptera; rejected ICZN Opinion 417) and *Herse* Hawle & Corda, 1847: 19 (Trilobita)).

Hyperia Gistel, 1848: VIII. Replacement name for *Cuvieria* Rang, 1827 (junior homonym of *Hyperia* Desmarest (ex Latreille MS), 1823: 347 (Crustacea)).

Cuvierina Boas, 1886: 131, 214 (replacement name for *Cuvieria* Rang, 1827 non Lesueur & Petit, 1807).

Rangistela Pruvot-Fol, 1948: 278. Unnecessary replacement name for ‘*Cuvierina*’ (*lapsus* for *Cuvieria*) Rang, 1827.

Urceolaria Janssen, 2005: 49. Type species (OD) *Cuvieria urceolaris* Mörcz, 1850: 32. Non *Urceolaria* Lamarck, 1801: Rotifera, non *Urceolaria* Stein, 1867: Ciliophora.

Urceolarica Janssen, 2006: 68 (replacement name for *Urceolaria* Janssen, 2005). Indian and Pacific oceans.

Description. Same as for family.

Distribution. Epi- to mesopelagic. Three species are represented in the North Pacific.

Remarks. Ever since Boas (1886) this genus was considered monotypic with only some formae or subspecies distinguished. Morphometric and molecular work, however, led to the distinction of six recent species (Janssen, 2005, Burridge *et al.* 2016). Two subgenera (Janssen 2005, 2006) based on differences in development interpreted as lineages of fossil species were rejected based on DNA data by Burridge *et al.* (2016).

***Cuvierina columnella* (Rang, 1827)**

(Figures 22, 23a–d)

Cuvieria columnella Rang, 1827: 323, pl. 45, figs B1–8. Neotype MNHN-IM-2000-33856 (Janssen 2005: 45, fig. 10). Marion Dufresne Expedition, MD32, SW Indian Ocean, 21°08.7'S 55°11.8'E.

Triptera rosea Quoy & Gaimard, 1825: 416, pl. 66, fig. 6 (soft parts only). No types available. Australia, near Port Jackson.

Cuvierina spoeli Rampal, 2002: 214, fig. 1A–Cs. Holotype MNHN-IM-2000-33848. Indian Ocean, 21°08' S, 55°11'E.

Description. Shell 7.1–11.1 mm, moderately inflated, longitudinal microornament present, aperture rounded triangular.

Distribution. In the eastern Pacific to ~20°N. In the northeastern Pacific only known from two specimens from 29°34'N 128°9'W (Fig. 20) in the Santa Barbara Museum of Natural History (SBMNH 133302, shell height 7.9 mm, width 2.7 mm, aperture height 1.25 mm, width 2.1 mm (Fig. 20) and shell height 8.1 mm, width 2.7 mm, aperture height 1.25 mm, width 2.1 mm). Rare.

Remarks. *Cuvierina spoeli* Rampal, 2002 was considered a synonym of *C. columnella* by Janssen (2007), which was rejected by Rampal (2017). The synonymy was again demonstrated by Janssen (2018a).

***Cuvierina tsudai* Burridge, Janssen & Peijnenburg, 2016**

(Figure 24)

Cuvierina tsudai Burridge, Janssen & Peijnenburg, 2016: 5, fig. 1A–I. Holotype RMNH.5004167. Pacific Ocean, 8°47'N, 158°49'W.

Description. Shell 7.2–8.8 mm, moderately inflated, no microornamentation, aperture triangular.

Distribution. In the northeastern Pacific to 37°N. Rare.

***Cuvierina urceolaris* (Mörch, 1850)**

(Figure 25a–b)

Cuvieria oryza Benson, 1835b: 698 (*nomen oblitum*: Janssen 2018a).

Cuvieria urceolaris Mörch, 1850: 32, pl. 1, fig. 8 (*nomen protectum*: Janssen 2018a). Lectotype NHMD-91674 (van der Spoel 1976: 191, fig. 5D). Philippine Islands, restricted to Bank Aguisan by van der Spoel (1976: 191).

Description. Shell 5.1–6.7 mm high, strongly inflated, microornament present, aperture reniform.

Distribution. Indian and Pacific Oceans, warm water species. From the northeastern Pacific recorded from off San Francisco (Rampal 2002: 212). Rare.

Cliidae Jeffreys, 1869

Cleodoridae Gray, 1840: 148, 155 (*nomen oblitum*: Bouchet & Rocroi 2005).

Cliidae Jeffreys, 1869: 118. ICZN 2006: Opinion 2133.

Clionae van der Spoel, 1967: 31, 57 (*partim*).

Clioidae auct. (incorrect subsequent spelling: Bouchet & Rocroi 2005).

Non Clioidae Menke, 1828: 5 (as *Cliodinae*), nowadays *Clionidae* (Gymnosomata).

Description. Shell conical to triangular, bilaterally symmetrical, straight or dorso-ventrally curved; ventral and dorsal shell parts separated by carinae, protoconch inflated, with or without apical spine; radial, transverse ornamentation present or absent.

Remarks. See note on the validity of this taxon under Cavolinioidea above.

***Clio* Linnaeus, 1767**

Clio Linnaeus, 1767: 1094. Type species (SD Gray 1847) *Clio pyramidata* Linnaeus, 1767. Caribbean Sea (Jamaica).

Cleodora Péron & Lesueur, 1810: 66. Type species (M) ‘*Cléodore Pyramidale*’ = *Clio pyramidata* Linnaeus, 1767. Type locality not given.

Euclio Bonnevie, 1913: 20 (objective junior synonym of *Clio*; van der Spoel 1967: 66).

Proclio Hubendick, 1951. Type species (M) *Proclio subteres* Hubendick, 1951 = *Clio antarctica* (Dall, 1908). South Atlantic, 48°27'S 42°36'W.

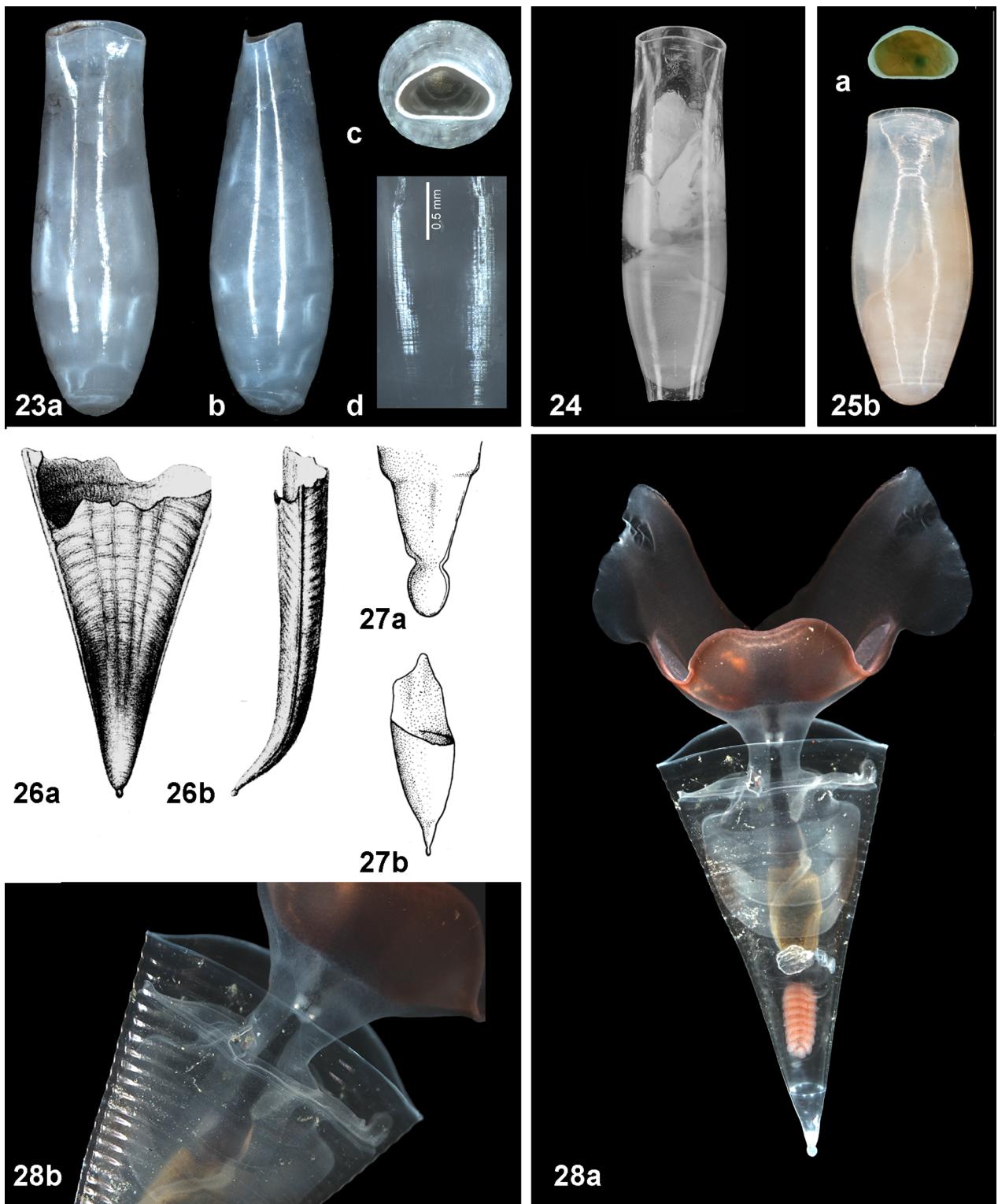
Description. Same as for the family.

Remarks. Since its introduction in 1810, the name *Cleodora* was generally used, as the name *Clio* was frequently utilized for shell-less pteropod species (Gymnosomata) that are today included in the genus *Clione* Pallas, 1774. Several other names introduced as (sub)genera in the Cliidae, such as *Balantium* Children, 1823 or *Bellardiclio* Janssen, 2004 as well as a number of names based on fossil species by Bellardi (1873) are currently not used in the WoRMS database.

***Clio andreae* (Boas, 1886)**

(Figures 26a–b, 27a–b, 28a–b)

Cleodora Andreae [sic] Boas, 1886: 80, 203, pl. 1, fig. 1; pl. 2, fig. 12; pl. 4, fig. 49; pl. 5, fig. 92. Holotype (nearly dissolved, shell fragments and soft parts) in NHMD-91479. Atlantic Ocean, 33°30'S, 11°E.



FIGURES 23–28. *Cuvierina*, *Clio*. **23a–d:** *Cuvierina columnella* (Rang, 1827). W of Guadelupe Island, California State, Fisheries Laboratory 65.S.3#2; 29°34'N 128°09'W; shell height 7.89 mm; 1 June 1965. SBMNH 133302. Photo by Ronald Pouwer. **24.** *Cuvierina tsudai*, Burridge, Janssen & Peijnenburg, 2016; holotype, Pacific Ocean, 8°47'N, 158°49'W; shell height 7.3 mm. RMNH 5004167 (courtesy of Alice K. Burridge). **25a–b.** *Cuvierina urceolaris* (Mörch, 1850). South China Sea, north of Philippines, DANA expedition, sta 3729(v), 20°3.5'N 120°50'E. Shell height 6.4 mm, NHMD collection (courtesy of Alice K. Burridge). **26a–b.** *Clio andreae* (Boas, 1886), holotype; South Atlantic Ocean, 33°30'S, 11°E (from Boas 1886) (left, shell height 20 mm) and what remains of it (from van der Spoel 1976) (right; sizes/magnification not given); NHMD-91479. **27a–b.** *Clio andreae* (Boas, 1886), holotype; South Atlantic Ocean, 33°30'S, 11°E (from Boas 1886) (left, shell height 20 mm) and what remains of it (from van der Spoel 1976) (right; sizes/magnification not given); NHMD-91479. **28a–b.** *Clio andreae* (Boas, 1886), Monterey Bay, California, collection depth 2556 m; shell height 40.6 mm. Photos by Stephanie L. Bush.

Description. Shell height to 20 mm, elongated triangular, apical angle ~25°, apical part curved dorsally; dorsal and ventral shell parts equally convex, dorsal shell part with three weakly developed longitudinal riblets; dorsal and ventral parts with transverse ribbing. Protoconch clearly separated, spherical, no apical spine.

Remarks. *Clio andreae* (Boas, 1886) was considered a senior synonym of *C. polita* Pelseneer, 1888 by van der Spoel (1976: 49, 191) based on fragments of the *C. andreae* holotype. However, Janssen (2012a: 49) preferred to consider both species as valid. Although very similar in shell shape, *C. andreae* has weak but distinct longitudinal and transversal ornament, whereas in *C. polita* both dorsal and ventral shell parts are unornamented.

Clio chaptalii Gray, 1850

(Figures 29a–d, 30a–c)

Clio chaptalii Gray, 1850: 14. Holotype MNHN-IM-2000-33847. Cape of Good Hope.

Description. Shell to 17 mm, triangular with straight sidelines, apical angle to almost 60°, curved dorsally in apical part. Dorsal shell part with three radial ribs; dorsal and ventral sides both with transverse ornament of numerous narrow riblets, curved in apertural direction.

Distribution. In northeast Pacific 53–59°N and 139–164°W. Epi- to bathypelagic species (100–1200 m). Rare.

Clio cuspidata (Bosc, 1802)

(Figures 31a–d, 32)

Hyalaea cuspidata Bosc, 1802: 241, pl. 9, figs 5–7. Syntypes probably present in MNHN, Paris, but unrecognizable as such by incomplete labeling (van der Spoel 1976: 191). ‘In ocean’.

Cleodora Lessonii Rang & de Féruccac, 1830: 261 (*nomen nudum*).

Cleodora quadrispinosa Lesson, 1831: 248, pl. 10, figs 1–1”, 2. Type material not available. Moluccas, 26°S 92°E.

Description. Shell to 20 mm high, lateral carinae strongly diverging, transverse section triangular, ventrally flattened with wide central swelling, dorsal shell part convex with sometimes strong central longitudinal rib; weaker ribs between central rib and lateral carinae; transverse ornament variably strong on both sides, following adaperturally curved growth lines. Lateral carinae, frequently also central dorsal rib elongated to apertural spines; protoconch spherical with distinct apical spine.

Distribution. In northeast Pacific to ~45°N. Epipelagic. Rare.

Clio polita Pelseneer, 1888

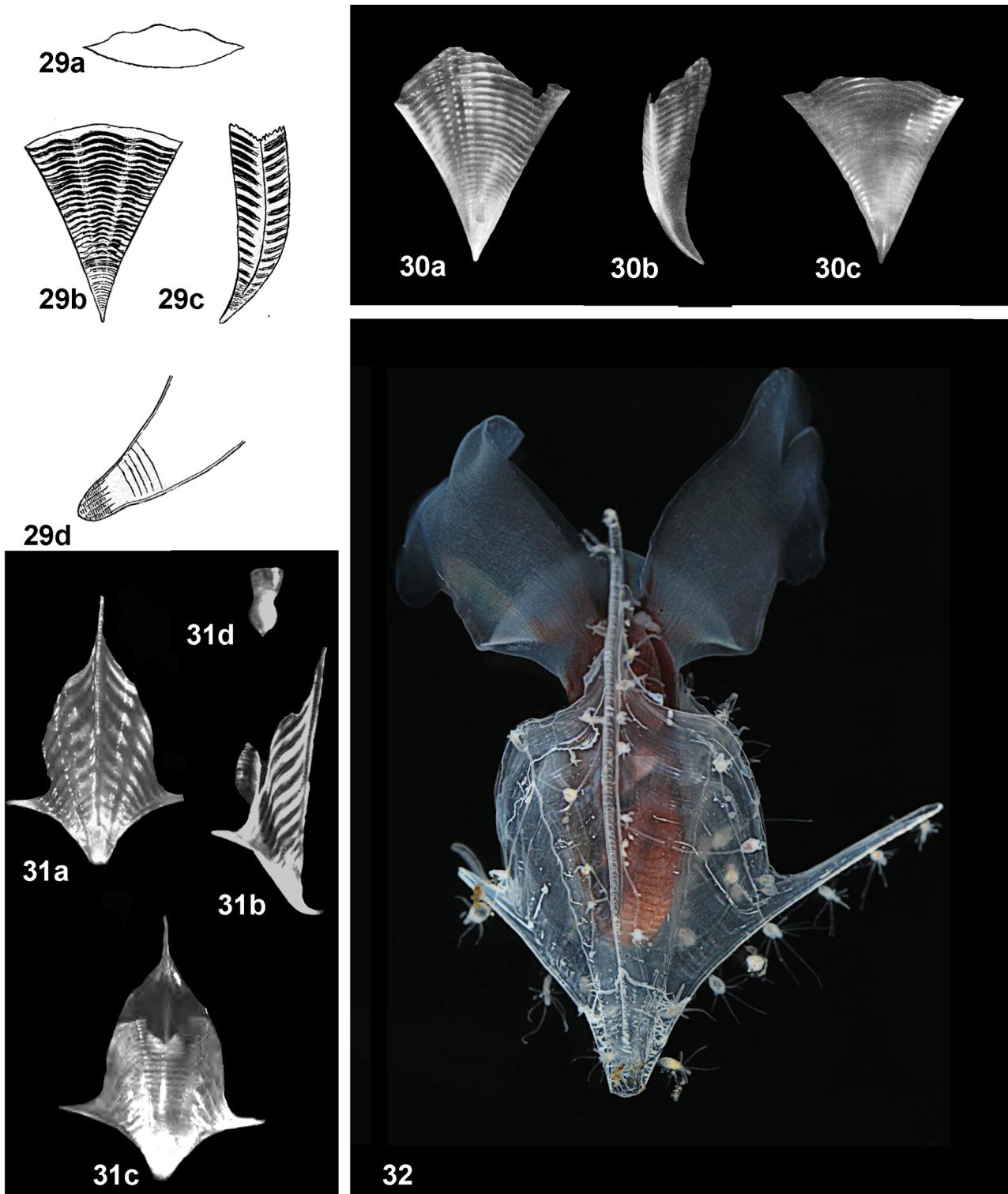
(Figures 33a–c, 34a–b, 35a–b)

Cleodora falcata Pfeffer, 1880: 96, figs 19, 19 a–b. Syntypes not in ZMH (non Gould, 1852).

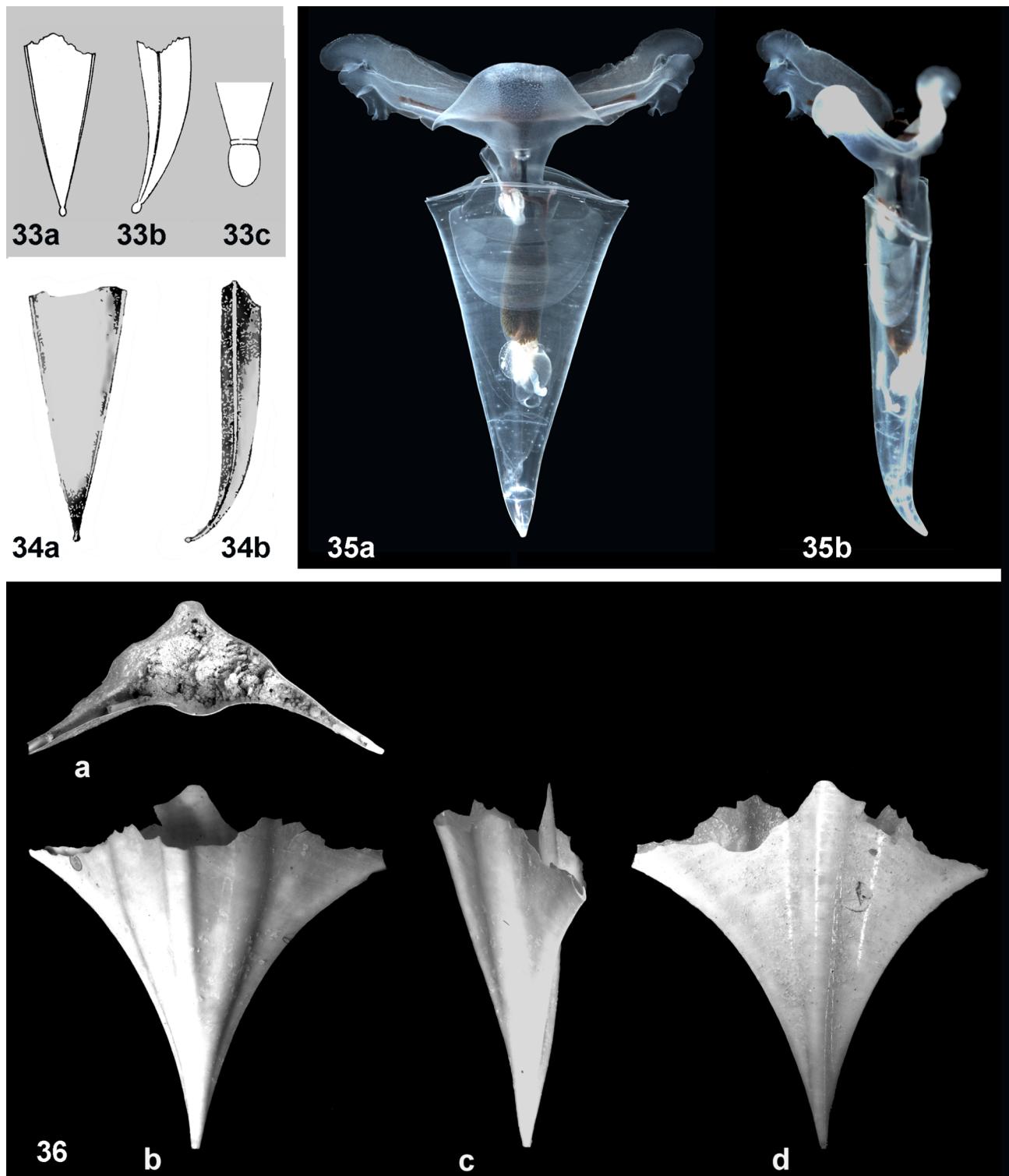
Clio polita Pelseneer, 1888: 60, pl. 2, figs 4–6. Syntypes lost. Several stations in the Atlantic Ocean.

Description. Shell height to ~22 mm, elongated triangular, apical angle ~25°, apical part curved dorsally; dorsal, and ventral shell parts convex, ventrally slightly more so, no ornamentation present. Carinae simple. Protoconch separated by distinct ring, globular, no apical spine.

Distribution. Bathypelagic species (> 1000 m). Predominantly Atlantic, only rarely reported from the north Pacific (McGowan 1960) between 150°W and 170°E, 40–53°N. McGowan’s specimens, however, consisted of the soft parts only, no shells, so it is unclear if they belonged to *C. polita* or *C. andreae*. Bé & Gilmer (1977) recorded *C. polita* from the Pacific (Gulf of Panama) and included McGowan’s records in their distribution map. They did not recognize *C. andreae*, but their illustration (pl. 6, fig. 16a–c) clearly represents that species. New material from the north Pacific is needed to clarify this situation. Three lots (USNM 857720, 857745, 857764) from the North Pacific (54–57°N, 141°W) are identified as *C. andreae*, but their shells are dissolved.



FIGURES 29–32. *Clio*. **29a–d.** *Clio chaptalii* Gray, 1850. Shell height c. 13 mm, locality not indicated (from Tesch 1946: pl. 3, fig. 13 [inverted]). **30a–c.** *Clio chaptalii* Gray, 1850. Shell height c. 17 mm, equatorial Atlantic (from Bé & Gilmer 1977). **31a–d.** *Clio cuspidata* (Bosc, 1802); Northern Atlantic Ocean, shell height 14.5 mm, protoconch (upper right) diameter 0.2 mm (from Bé & Gilmer 1977). **32.** *Clio cuspidata* (Bosc, 1802), colonized by the hydroid *Pandea* sp. Monterey Bay, California; shell height 7 mm. Photo by Stephanie L. Bush.



FIGURES 33–36. *Clio*. 33a–c. *Clio polita* Pelseneer, 1888. Shell height given as 10–11 mm. Atlantic Ocean (from Pelseneer 1888). 34a–b. *Clio polita* Pelseneer, 1888, Atlantic Ocean; shell height 12.5 mm (from Pfeffer 1880 as *Cleodora falcata* Pfeffer, 1880, syntypes). 35a–b. *Clio polita* Pelseneer, 1888, ventral (left) and left lateral (right) views. Monterey Bay, California; collected at depth 1,117 m, shell height 21.54 mm. Photos by Stephanie L. Bush. 36a–d. *Clio pyramidata* Linnaeus, 1767. Neotype, RGM 777 444. Jamaica, East Channel, bottom sample nr Est 875F, leg. Ivan Goodbody, R/V Eastward, 17 February 1972; shell height 11.4 mm; a: apertural, b: dorsal, c: right lateral, d: ventral views (from Janssen *et al.* 2018).

***Clio pyramidata* Linnaeus, 1767**

(Figures 36a–d, 37, 38a–b)

? *Clio caudata* Linnaeus, 1767: 1094. No syntypes available. Type locality ‘*in oceano*’.

Clio pyramidata Linnaeus, 1767: 1094. Neotype RGM 777 444. Caribbean Sea, Jamaica (Janssen *et al.* 2018: 96).

Clio retusa Linnaeus, 1767: 1094. No syntypes available. Type locality ‘*in oceano*’.

Hylaea lanceolata Lesueur, 1813: 284, pl. 5, fig. 3. Syntypes not present in Paris Museum (van der Spoel, 1976: 190).

Mediterranean, off Nice.

? *Cleodora brownii* de Blainville, 1825: 481, pl. 46bis, figs 1, 1a–b). Types unknown. Type locality not mentioned.

Clio exacuta Gould, 1852: 488; 1856: pl. 51, fig. 605a–b. Syntypes were not located by Johnson (1964: 73). Pacific Ocean, 44°N, 154°W.

Clio occidentalis Dall, 1871: 140. Types unknown. Pacific Ocean, off California coast, 33°N, 130°W.

Cleodora sulcata Pfeffer, 1879: 240, figs 11–12. Syntypes probably in Museum für Naturkunde, Berlin, Germany, not in the Zoologisches Museum, Hamburg, Germany (as stated by van der Spoel, 1976: 190). South Atlantic Ocean; 45°53,9'S 122°1,1'W; 50°34,6'S 83°44,5'W; Kerguelen.

Cleodora martensi Pfeffer, 1880: 95, figs 16, 16a–c. Lectotype and paralectotype (van der Spoel 1976: 190) ZMH 3013-3014. Atlantic Ocean.

Clio antarctica Dall, 1908: 501 (replacement name for *Hylaea australis* d’Orbigny, 1836: 117, pl. 8, figs 9–11 *non Clio australis* Bruguière, 1792: 507, pl. 75, figs 1–2 = *Clione limacina* (Phipps, 1774) *nec Hylaea australis* Péron & Lesueur, 1807: pl. 31, fig. 5 = *Cavolinia tridentata* (Forsskål *in* Niebuhr, 1775). Syntypes not in MNHN. ‘Du cap Horn, par 57 degrés 10 minutes de latitude sud, et 70 degrés de longitude ouest de Paris’.

? *Proclio subteres* Hubendick, 1951 = *Clio antarctica* (Dall, 1908). Holotype in ZMS. South Atlantic, 48°27'S 42°36'W.

Description. Shell straight, lateral carinae diverging, apical angle strongly increasing towards aperture, carinae simple, transverse section initially circular, becoming triangular towards aperture, dorsal shell part with strong central longitudinal rib, lateral ribs weaker, ventral shell part slightly concave laterally with weak, wide central swelling, apertural margin simple, dorsally triangularly protruding, ventrally lower, rounded, protoconch pear-shaped, separated by constriction, sharply pointed.

Distribution. In the northeast Pacific to 60°N. Eurythermal, meso- to epipelagic. Common to ~40°N, uncommon but present to 60°N.

***Clio recurva* (Children, 1823)**

(Figures 39a–b, 40a–d, 41a–d, 42)

Balantium recurvum Children, 1823: 220, pl. 7, fig. 107. Syntypes in NHMUK? ‘Congo expedition ‘(Gulf of Guinea?)’.

Cleodora balantium Rang, 1834: Class V, pl. 44. Type material unknown. Golfe du Guinée, near Cap de Palame.

Description. Largest species in the genus (shell height to 30 mm), straight longitudinally, but apical shell part curved dorsally, lateral carinae double-lined, somewhat flexuous in apical part, very slightly convex adaperturally. Both sides of shell convex, dorsal side with three radial ribs, middle one stronger, ventral side with single, wide swelling. Transverse ornament of numerous curved ripples on both sides. Protoconch clearly separated, spherical, with distinct (but easily worn) apical spine.

Distribution. In northeast Pacific 30–45°N. Meso- to bathypelagic (300–2500 m), rare, but occasionally collected from the sea surface.

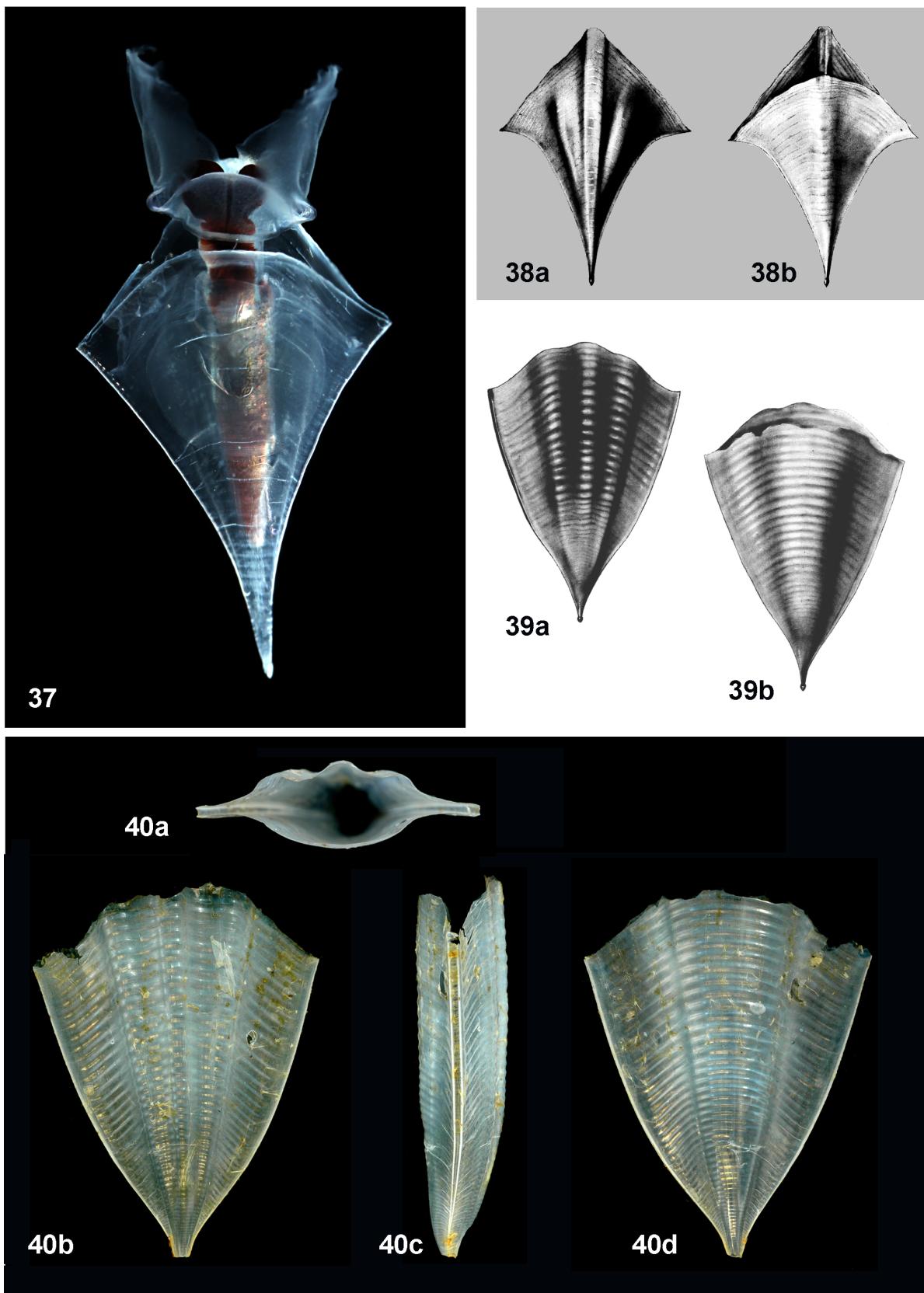
Remarks. Shells of living specimens are frequently encrusted with hydroids.

Cavoliniidae Gray, 1850 (1815)

Hyalinea Rafinesque, 1815: 140 [ICZN Art. 40(2)].

Cavoliniidae Gray, 1850: 3.

Cavoliniidae Official List of Family Group Names in Zoology, nr 438.



FIGURES 37–40. *Clio*. **37.** *Clio pyramidata* Linnaeus, 1767 Monterey Bay, California; shell height 8.5 mm. Photo by Stephanie L. Bush. **38a–b.** *Clio pyramidata* Linnaeus, 1767. California. Shell height 9.3 mm; left: dorsal view; right: ventral view (from McGowan 1968). **39a–b.** *Clio recurva* (Children, 1823). California, shell height 18.5 mm (from McGowan 1968). **40a–d.** *Clio recurva* (Children, 1823). 0 m, 475 mi W of Point Sur, California; 36°18'N 131°44'W, shell height 23.3 mm (SBMNH 457571). Photo by Ronald Pouwer.

Description. Ventral and dorsal shell parts convex, separated by lateral slits (*Cavolinia*, *Diacavolinia*) or carinae (*Diacria*), dorsal side with radial ornament, higher than more convex ventral side with only fine transverse ornamentation, dorsal lip with thickened margin (*Diacria*) or overhanging aperture (*Cavolinia*, *Diacavolinia*), ventral apertural margin curved outward, apical spine with protoconch either straight or curved dorsally, pointed, with transverse microornamentation (*Cavolinia*), or straight and with apical bulb; shed in some species, then opening subsequently closed by septum, or apical shell parts always missing (*Diacavolinia*).

Remarks. The authority of some species in Cavoliniidae originally described in the genus *Hyalaea* in the work of de Blainville (1821a, b) (e.g., *Diacavolinia longirostris* and *Diacria trispinosa*) has also been given erroneously as Lesueur, 1821 (e.g. WoRMS). De Blainville (1821a: 79) wrote “On doit la connaissance et la distinction de la plupart des espèces de ce genre, à MM. Péron et Lesueur, et surtout à ce dernier, qui en a fait une monographie avec figures, dont le manuscrit m'a été confié” [One owes the knowledge and the distinction of the majority of the species of this genus to MM. Péron and Lesueur, and certainly to the latter, who has made of it a monograph with figures, of which the manuscript was entrusted to me.] Accordingly, the description is based on a Lesueur manuscript, which makes the authority of those taxa de Blainville, ex Lesueur MS. As Lesueur's text was not copied verbatim, the authority is not Lesueur *in de Blainville* (ICZN Art. 50.1 Example).

***Cavolinia* Abildgaard, 1791**

Cavolina Abildgaard, 1791: 175 (emended ICZN 1969 Opinion 883; Official List name nr 1841). Type species (M) *Cavolina natans* Abildgaard, 1791 = *Cavolinia tridentata* Forsskål in Niebuhr, 1775.

Hyalaea Lamarck, 1801: 139. Type species (M) *Hylaea cornea* Lamarck = *Cavolinia tridentata* (Forsskål in Niebuhr, 1775). Tropics and subtropics worldwide.

Pleuropus Eschscholtz, 1825: 735, pl. 5, fig. 2. Type species (M) *Pleuropus pellucidus* Eschscholtz, 1825 = *Cavolinia inflexa* (Lesueur, 1813). ‘Südsee’ [southern ocean].

Orbignya Adams, 1859: 45. Type species (here designated) *Cavolina* (*Orbignya*) *labiata* d'Orbigny. Atlantic and Indian oceans.

Archonta de Montfort, 1810: 50–51. Type species (M) *Archonta exploratus* Montfort, 1810 = *Cavolinia inflexa* (Lesueur, 1813). ‘Fort-Blanc à l'est du port de Dunkerque’, Belgium.

Description. Ventral and dorsal shell parts only connected to each other in basal part, separated by lateral slits, dorsal lip overhanging aperture, apertural margins not thickened, closing mechanisms present on both sides between aperture and lateral slit; apical spine with protoconch curved dorsally, pointed, with transverse microornamentation; sometimes shed, opening closed by septum.

Remarks. Although the generic name *Orbignya* is not currently used, the group of taxa related to *Cavolinia inflexa* (Lesueur, 1813) as distinguished by Rampal (2002) is so homogeneous and different from *Cavolinia*, *sensu stricto* that ongoing integrative morphological and molecular work is expected to result in a separate status of this group. Therefore, it is thought useful to designate a type species. Adams (1859) included two species in *Orbignya*, ‘*C. inflexa*, Lesueur’ and ‘*C. labiata* D’Orb.’. Designation of *C. inflexa* as type species would make it a junior synonym of *Pleuropus* Eschscholtz, 1825. Therefore, *C. labiata* is here chosen as the type species of *Orbignya*.

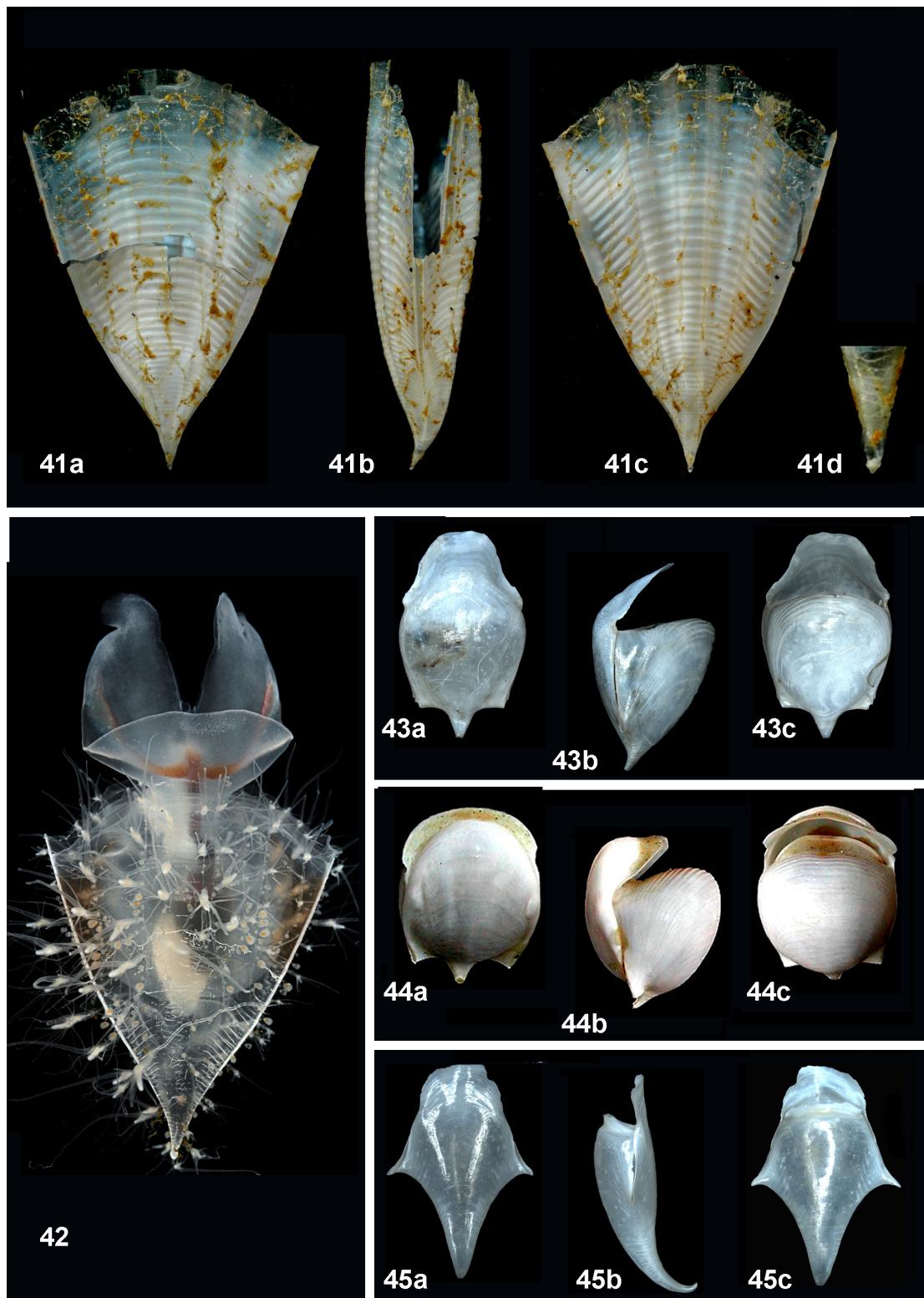
***Cavolinia gibbosa flava* (d'Orbigny, 1835)**

(Figure 43a–c)

Hyalaea flava d'Orbigny, 1835: 97, pl. 5, figs 21–25. Holotype NHMUK 1854.12.4.13. Pacific Ocean 30°S, 92°E.

Pleuropus hargeri Verrill, 1882: 555. No syntypes known. West Atlantic Ocean, George's Bank, 41°25'N, 65°5' to 65°30'W.

Description. Shell height to 11 mm, dorsal shell part with five, sometimes rather weakly developed radial ribs, dorsal apertural lip overhanging aperture at angle of ~45° respective to shell vertical axis; ventral shell part not regularly convex as in most *Cavolinia* species, but with clear, rounded angularity above mid shell height, fine transverse lirae on most convex part.



FIGURES 41–45. *Clio*, *Cavolinia*. **41a–d.** *Clio recurva* (Children, 1823). Off Central California, 0 m, 36°30'N 130°30'W, shell height 21.2 mm (SBMNH 116445). The brown patches are hydroid remnants (compare Fig. 42); shell height 21 mm. Photo by Ronald Pouwer. **42.** *Clio recurva* (Children, 1823), shell height 11 mm, colonized by the hydroid *Pandeia* sp. Monterey Bay. Photo by Stephanie L. Bush. **43a–c.** *Cavolinia gibbosa flava* (d'Orbigny, 1834). Between California and Hawaii, from stomach of *Alepisaurus*, 27°41'N 135°3'W, shell height 10.79 mm (SBMNH 124733). Photo by Ronald Pouwer. **44a–c.** *Cavolinia globulosa* (Gray, 1850), shell height 5 mm. Hawaii, south west of Kaula Rock; Vanderbilt Pacific Equatorial Expedition; 1951 from website: <http://seaslugsofhawaii.com/species/Cavolinia-globulosa-a.html>; photographed at CAS (courtesy of Cory Pittman). **45a–c.** *Cavolinia inflexa imitans* (Pfeffer, 1880). Off La Jolla, San Diego County, California, USA, 32°49'59.995"N, 117°16'0.013"; shell height 6.2 mm (SBMNH 457570). Photo by Ronald Pouwer.

Remarks. Typical *C. gibbosa* is smaller (to c. 7.5 mm shell height), with a more sharply vaulted ventral shell part, and dorsal apertural lip and apical spine with protoconch more strongly curved. These two taxa, and two additional ones, *C. plana* Meisenheimer, 1905, described from the eastern Indian Ocean, and *C. gibboides* Rampal, 2002, from the eastern Mediterranean, are usually interpreted as forms or subspecies, but Rampal (2002) considered them to be distinct species (see Janssen 2012a, Rampal, 2014).

Distribution. Epipelagic, mainly bisubtropical, warm water species with a patchy distribution. Known in the northeast Pacific Ocean from c. 45°N and east of 175°W. Rare.

Cavolinia globulosa (Gray, 1850)

(Figure 44a-c)

Cavolina globulosa Gray, 1850: 8. Lectotype (van der Spoel, 1976: 196) MNHN-IM-2000-33899. ‘Nouvelle Hollande’ [= Australia].

Description. Shell height to approximately 6 mm, spherical with largest shell width at mid height, above small lateral spines; dorsal shell part with five, rather weak radial ribs, dorsal apertural lip strongly curved ventrally, overhanging aperture; ventral shell part very convex, regularly rounded to sometimes very slightly angular, with clear transverse lirae on most convex part.

Distribution. In northeast Pacific to about 40°N. Epi- to mesopelagic (~ 600 m). Rare.

Cavolinia inflexa imitans (Pfeffer, 1880)

(Figures 45a–c, 46)

[*Hyalea*] Gruppe *inflexa*, Form A. *imitans* Pfeffer, 1880: 90, pl. 7, fig. 9a. Lectotype ZMH 2972, paralectotypes ZMH 2973-2974, 71037 (van der Spoel, 1976, paralectotype fig. 55D). Atlantic Ocean and Zanzibar.

Description. Less spherical, more elongate than other species of genus; apical shell part below lateral spines relatively large, reaching half shell height or slightly less, dorsal shell part with three weakly developed radial ribs only central one of which sometimes well-visible, dorsal lip rounded, not deviating from long axis; ventral side gradually convex, smooth; ventral apertural lip clearly separated by transverse groove; apical spine curved dorsally.

Remarks. The *C. inflexa* species complex has been the subject of several taxonomic interpretations (Boas 1886, van der Spoel, 1967, Rampal, 2002). Various related forms (or subspecies?) were described, of which three seem to be accepted presently: *inflexa*, *imitans* (Pfeffer, 1880) and *labiata* (d’Orbigny, 1835), each of these being treated as independent species, subspecies, or forma in the literature.

Distribution. In the northeast Pacific the species is found between 20 and 40°N. All specimens seem to belong to the form *C. inflexa imitans*. Meso- to epipelagic (200–800 m). Common.

Cavolinia tridentata (Forskål in Niebuhr, 1775)

(Figures 47a–c, 48a–c)

Monoculus telemus Linnaeus, 1758: 635. Genus and species suppressed (ICZN Opinion 288). Official Index of Rejected and Invalid Specific Names in Zoology nr 72.

Anomia tridentata Forskål in Niebuhr, 1775: 124. Official List of Specific Names in Zoology, name number 119. Syntypes? Mediterranean Sea.

Cavolinia natans Abildgaard, 1791: 175. Type material not available. Mediterranean.

Hyalaea cornea Lamarck, 1801: 140. Type material not available. Mediterranean.

Hyalaea papilionacea Bory de St. Vincent, 1804: 138, pl. 5, fig. 1A –F. Type material unknown. West Africa.

Hyalaea australis Péron & Lesueur, in Péron, 1807: 46, pl. 31, fig. 5. Type material not available. Type locality. ‘Océan Austral’.

Hyalaea chemnitziana Lesueur, 1813: 284. Name based on *Anomia alata et aurita scarabaeiformis* Martini & Chemnitz, 1785: 72, vignette 13, figs G–F. No locality indicated.

Hyalaea peronii Lesueur, 1813: 284. Type material not available. Mediterranean.

Hyalaea teniobranchea Lamarck, 1816: 13, pl. 464, fig. 7. Type material not available. Location not indicated.

Hyalaea forskahlii de Blainville, 1821a: 79 (*nomen nudum*); 1821b: 95. Type material not available. Mediterranean.

Hyalea rangii Deshayes, 1832: 310. Type material not available. ‘des mers d’Afrique’.
Hyalaea affinis d’Orbigny, 1835: 91. Type material not available. Pacific Ocean, 30–34°S, 80–92°W (of Paris).
Hyalea melly Benoit, 1843: 4. Type material not available. Forte del Salvadore, Sicily (Italy).
Pleuropus longifilis Troschel, 1854: 202, pl. 8, figs 1–3. Type material not available. Near Messina, Sicily (Italy).
Cleodora trifilis Troschel, 1854: 205, pl. 8, fig. 4. Type material not available. Sicily (Italy).
Hyalea [sic] complanata Gegenbaur, 1855: 40, pl. 1, figs 1–4. Type material not available. Near Messina, Sicily (Italy).
Hyalaea cumingii G.B. Sowerby II, 1878: caption of Pteropoda pl. 1, fig. 5a–b. Syntypes in NHMUK ? Origin not mentioned.
Cavolina occidentalis Dall, 1908: 233, pl. 12, fig. 1, 1b. Holotype USNM 110591, paratypes USNM 110590. North Pacific Ocean, 38°4'N, 137°W.

Description. Shell large (in the northern Pacific height up to 14 mm), spherical, brownish, lateral spines short, somewhat curved downward, dorsal apertural lip well separated, rounded, ventral shell part swollen, with clear transverse striae close to curved apertural margin; apical spine with protoconch pointed, straight, not curved dorsally.

Distribution. In northeast Pacific disjunct distribution to ~50°N, but occasionally occurring to 67°N. Epipelagic. The northeast Pacific population is usually referred to as forma *affinis* (d’Orbigny, 1835). Common.

Cavolinia uncinata (d’Orbigny, 1835)

(Figures 49a–c, 50)

Hyalea uncinata Rang, 1829: 114. Lectotype MNHN-IM-2000-33898 (van der Spoel 1976: 195). Atlantic Ocean (*nomen nudum*).

Hyalaea uncinata Rang. D’Orbigny, 1835: 93; 1835: pl. 5, figs 11–15.

? *Hyalea uncinata* form B *uncinatiformis* Pfeffer, 1880: 83. Syntypes ZMH 3180–3185. Atlantic Ocean.

Description. Shell resembling *C. tridentata* in shape, but relatively wider, height less than 10 mm, only faintly colored brownish, usually colorless (clear). Dorsal shell part with five radial ribs, stronger than in *C. tridentata*. Dorsal apertural lip more strongly overhanging aperture. Lateral spines well-developed, pointing downward, apical spine with protoconch strongly curved backward, its initial part perpendicular to shell’s vertical axis.

Distribution. In northeast Pacific to 30°N–40°N (Dall 1889, Abbott 1954, McGowan 1960, Bé & Gilmer 1977). Epipelagic. Uncommon.

Remarks. Although frequently cited with the authorship of Rang (1829) that author did not describe the species, but merely mentioned the name as an example for the genus *Hyalaea*. Rang illustrated the species (1829: pl. 2, fig. 2) but without a name (Gofas 2018). D’Orbigny (1835) validly introduced the taxon. As d’Orbigny referred to Rang’s paper we consider Rang’s material to be syntypes and the lectotype designation of van der Spoel (1976) as valid.

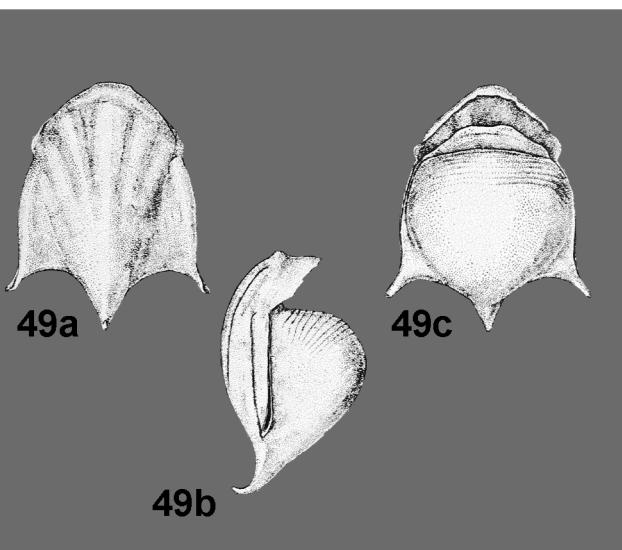
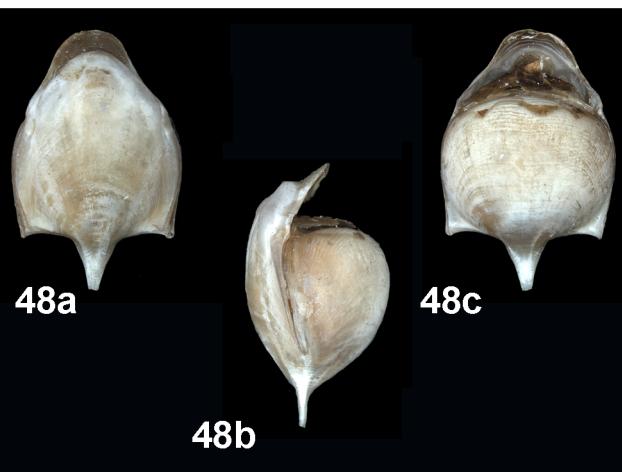
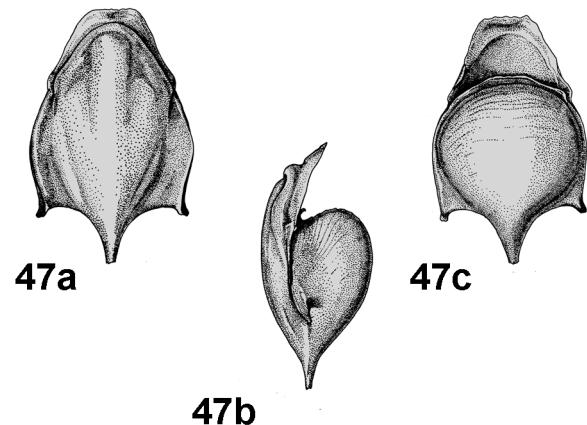
Van der Spoel (1969, 1971) introduced several formae in *C. uncinata*, based on small shell characteristics or color pattern. These names are nomenclaturally invalid, being published after 1961 (ICZN Art. 10.2). The form represented in the northeast Pacific agrees with f. *pulsata* van der Spoel, 1969.

Diacavolinia van der Spoel, 1987

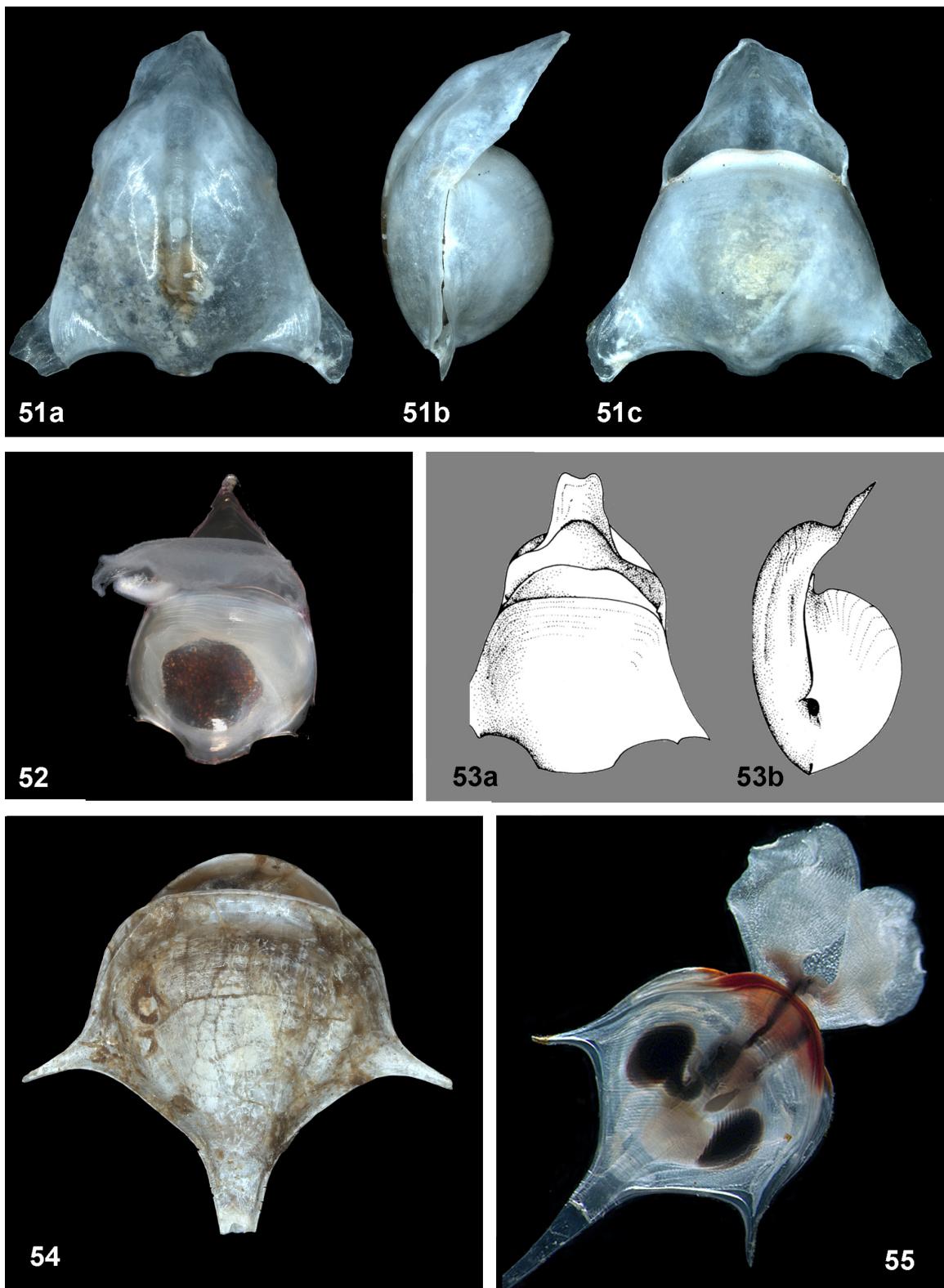
Diacavolinia van der Spoel, 1987: 78. Type species (OD) *Diacavolinia longirostris* (de Blainville, ex Lesueur MS 1821b). Atlantic Ocean.

Description. Differing from *Cavolinia* by second interlock system on both sides of aperture (only one in *Cavolinia*), apical spine with protoconch shed in adult specimens, opening closed with septum or fusion of ventral and dorsal shell parts.

Remarks. The taxonomy of *Diacavolinia* is unresolved. Numerous taxa have been introduced (van der Spoel 1970, 1971, 1973, van der Spoel *et al.* 1993) that are considered either forms or species, but are difficult to distinguish genetically (Maas *et al.* 2013).



FIGURES 46–50. *Cavolinia*. **46.** *Cavolinia inflexa imitans* (Pfeffer, 1880), Monterey Bay, California; shell height 6 mm. Photo by Stephanie L. Bush. **47a–c.** *Cavolinia tridentata* (Forskål in Niebuhr, 1775); shell height 14 mm. California, from McGowan (1968). **48a–c.** *Cavolinia tridentata* (Forskål in Niebuhr, 1775). Between California and Hawaii, from stomach of *Alepisaurus*, 27°41'N 135°3'W, shell height 9.5 mm (SBMNH 124733). Photo by Ronald Pouwer. **49a–c.** *Cavolinia uncinata* (d'Orbigny, 1834); shell height 7.4 mm, California (from McGowan, 1968). **50.** *Cavolinia uncinata* (Rang, 1829). Locality and size not given. Courtesy of Russell R. Hopcroft.



FIGURES 51–55. *Diacavolinia*, *Diacria*. **51a–c.** *Diacavolinia* aff. *longirostris* (de Blainville, ex Lesueur MS, 1821); 3–4 fms, Bahia San Luis Gonzaga, Baja California (Norte), Mexico, 29°47'N 114°20'W; shell height 5.8 mm (SBMNH 127831). Photo by Ronald Pouwer. **52.** *Diacavolinia* aff. *longirostris* (de Blainville, ex Lesueur MS, 1821); Gulf of California; shell height 6 mm. Photo by Stephanie L. Bush. **53a–b.** *Diacavolinia pacifica* van der Spoel, Bleeker & Kobayasi, 1993. Snellius II expedition, sta. 33 cast 2, 06°29.9'S, 131°09.2'E; shell height 4.40 mm. (Holotype ZMA.MOLL.137628. From van der Spoel *et al.* (1993: fig. 15A–B). **54.** *Diacria major* (Boas, 1886). Between California and Hawaii, from stomach of *Alepisaurus*, 33°39'N, 135°W, shell height 9 mm. SBNH 124724. Photo by Ronald Pouwer. **55.** *Diacria major* (Boas, 1886), from <http://www.ma-zaika.ru/post103199767/>; locality and size not indicated. Courtesy of Russell R. Hopcroft.

***Diacavolinia* aff. *longirostris* (Blainville, ex Lesueur MS, 1821)**

(Figures 51a–c, 52)

Hyalaea longirostris de Blainville, ex Lesueur MS, 1821b: 81. Type material not available in MNHN (van der Spoel 1976: 193). ‘Océan atlantique par 22°9' de latitude, a trois lignes de long sur deux de large’. Van der Spoel *et al.* (1993: fig. 38) interpreted this as western central Atlantic Ocean.

Description. Same as for genus.

Distribution. In northeast Pacific from 29°N (SBMNH 127831). Epipelagic. Rare.

Remarks. Using van der Spoel *et al.*'s (1993: 149) identification key did not lead to a confident identification of the *Diacavolinia* specimens recorded here (Figs 48, 49) from the northeast Pacific. Therefore, herein they are indicated as *D. aff. longirostris*. It should be noted, however, that they do not at all resemble the single *Diacavolinia* species recognized for this area by van der Spoel *et al.* (1993), which was *D. pacifica* van der Spoel *et al.*, 1993 (Figure 53a–b herein), a form distinguished by a distinct ‘dorsal hump’ (Fig. 53b), contrary to the available specimens, in which the lip is gradually connected to the dorsal shell part.

***Diacria* Gray, 1840**

Diacria Gray, 1840: 155. Type species (SD Gray 1847: 203) *Hyalaea trispinosa* de Blainville, ex Lesueur MS, 1821. Tropical and subtropical seas worldwide.

Description. Shell of two main shapes: 1) rhombic, dorso-ventrally flattened with long but frequently broken apical spine, spherical protoconch, lateral spines well-developed (*D. trispinosa*-group); 2) shell rather spherical, cavoliniform, apical spine with elliptical protoconch shed during metamorphosis, opening closed by septum, lateral spines small (*D. quadridentata*-group).

Remarks. The various forms and species introduced in the genus *Diacria* based on shell morphology (mainly measurements or color patterns) require re-assessment. Here, the species classification accepted in the WoRMS database is used.

Species of the *Diacria trispinosa* (de Blainville, ex Lesueur MS, 1821)-group

Description. Shell rhombic, dorso-ventral diameter less than half shell width, lateral spines well-developed, protoconch spherical, usually not shed but frequently broken. Dorsal shell part with five subequal radial ribs, ventral part with wide central rib, narrow lateral ones.

***Diacria major* (Boas, 1886)**

(Figures 54–55)

Hyalaea trispinosa var. *major* Boas, 1886: 95, 210. Lectotype (van der Spoel 1976: 293) NHMD-189947, but number given in absentia (the specimen not found present Sep. 2017; some paralectotypes in alcohol present; T. Schiøtte, pers. comm.). Lectotype locality 25°N, 35°30'W (Atlantic Ocean).

Description. Shell height to approximately 13 mm, lateral spines pointing downwards. Dorsal shell part above lateral spines as high as wide or higher; higher than in *D. trispinosa*.

***Diacria trispinosa* (de Blainville, ex Lesueur MS, 1821)**

(Figure 56a–c)

Hyalaea trispinosa de Blainville, ex Lesueur MS, 1821b: 97. Syntypes not found in MNHN (van der Spoel 1976: 193). 15°58'N, 56°44'W (of Paris ?) (= central western Atlantic).

Hyalaea mucronata Quoy & Gaimard, 1827: 231, pl. 8B, figs 1–2. Type material not available. Gibraltar, near Ceuta.

Hyalaea depressa Bivona Bernardi, 1832: 57. No syntypes available. Mediterranean.

? *Cleodora infundibulum* Wood, 1842: 459, pl. 5, fig. 13. Holotype (apical fragment) NHMUK G. 6896. Sutton, U.K. (Pliocene).

Cleodora compressa Souleyet, 1852: 51. Syntypes in NHMUK (Gray 1855: 7). Atlantic Ocean.

- Cavolinia reeveana* Dunker, 1853: 2. Type material not available. ‘Sinu Guineensi’ (= Gulf of Guinee, W. Africa).
- Hyalaea trispinosa* var. *minor* Boas, 1886: 95. A single certain syntype NHMD-189942. Atlantic and Indian oceans.
- Diacria rampali* Dupont, 1979: 39, fig. 3. Holotype NHMD-91487. Caribbean Sea 16°06'N, 76°02'W (Dana expedition sta. 1215 IV).
- Diacria piccola* Bleeker & van der Spoel, 1988: 60, figs 2–4. Holotype USNM 276782, paratype USNM 859098. Philippines, off Magavao Island, Mindanao, 8°50'45"N, 126°26'52"E.
- Diacria maculata* Bleeker & van der Spoel, 1988: 61, figs 8–9. Holotype USNM 283052, paratypes USNM 859099. Philippines, Lagonbnoy Gulf, E. Luzon, 13°37'30"N, 123°41'09"E.
- Diacria rubecula* Bontes & van der Spoel, 1998, 81. Holotype ZMA 398011, paratypes ZMA 398012 (now in RMNH). 48°58.9'N, 30°1.3'W.
- Diacria atlantica* Dupont in Bontes & van der Spoel, 1998: 81. Holotype NHMD-189678. 39°21'N, 21°51'W.
- Diacria gracilis* Rampal, 2002: 249, figs 21A–H, K; 23E–G. Holotype MNHN-IM-2000-33867. Western Pacific Ocean, 2°27'S, 169°38'E.
- Diacria trispinosa heterocolorata* Rampal, 2002: 247, figs 20A–C, 23C. Holotype MNHN-IM-2000-33863. Mozambique Canal, 11°31'S, 47°23'E.

Description. Shell to approximately 11 mm high, lateral spines perpendicular to shell's long axis. Dorsal shell part above lateral spines wider than high, wider than in *D. major*.

Distribution. In northeast Pacific to ~40°N, more commonly found in the southern parts. Uncommon.

Species of the *Diacria quadridentata* (de Blainville, ex Lesueur MS, 1821)-group

Description. Shell cavoliniform, dorso-ventral diameter more than half shell width, dorsal, especially ventral shell parts convex, lateral spines small to insignificant, protoconch elliptical, shed during metamorphosis.

Remarks. The typical species of the group is from the tropical Indo-Pacific.

Diacria danae van Leyen & van der Spoel, 1982

(Figures 57a–c, 58a–b)

Diacria quadridentata (de Blainville, ex Lesueur MS, 1821) forma *danae* van der Spoel, 1968: 217, fig. 1A–C. [unavailable infrasubspecific name]

Diacria danae van Leyen & van der Spoel, 1982: 112. Holotype NHMD-189860, but number given in absentia (the specimen not found present Sep. 2017; T. Schiøtte pers. comm.). 2°57'S, 99°36'E (eastern Indian Ocean).

Description. Shell height to ~2.1 mm, H/W ratio c. 1.25, dorsal shell part with five vaguely indicated radial ribs, three transverse riblets anticipating dorsal apertural margin, distance between lateral spines almost same as total shell width; thickened apertural margins brown colored in fresh specimens. Scar of apical spine 0.50–0.72 mm wide.

Remarks. No northeast Pacific specimens known to us; but occurring to 30°N (van Leyen & van der Spoel 1982: fig. 8). Epipelagic. Rare?

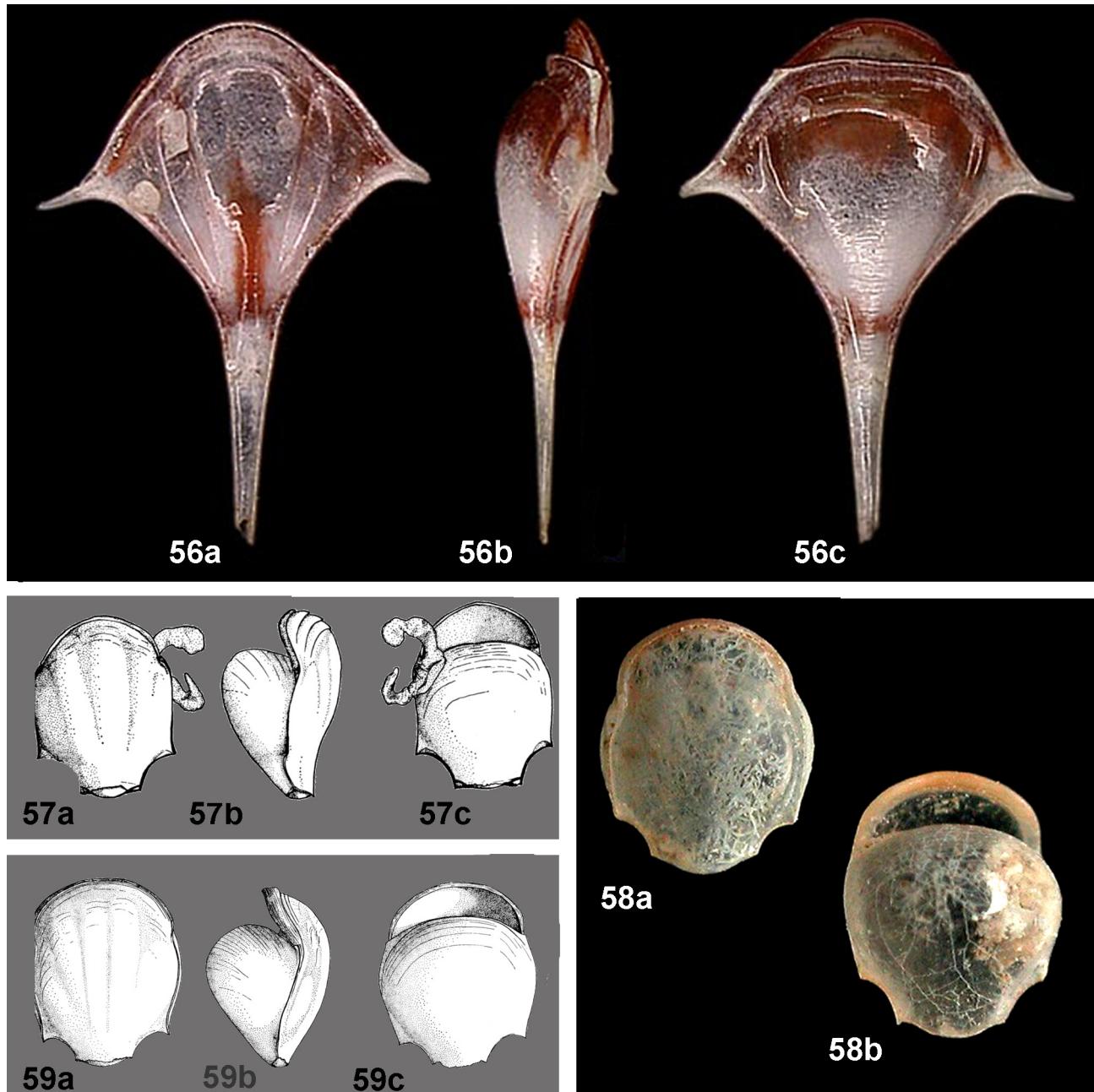
Diacria schmidti van Leyen & van der Spoel, 1982

(Figure 59a–c)

Diacria schmidti van Leyen & van der Spoel, 1982: 113. Holotype NHMD-91521, 4°20'S 116°46'W (tropical east Pacific).

Description. Shell hright to ~4.5 mm, H/W-ratio c. 1.20, distance between lateral spines c. 4/5th of total shell width; spines curved downward; apical spine scar between 1.16 and 1.36 mm wide; two or three transverse striae anticipating dorsal. Fresh specimens light brown all over.

Distribution. Epipelagic. In northeast Pacific to 28°N, but in the distribution map of van Leyen & van der Spoel (1982: fig. 8) this species is restricted to the tropical Pacific between approcimately 12°S and 20°N. Lots from two Velero stations with single specimen each in LACM (1941-30.2, LACM 1949-236.1) were collected further north: 28°17.3'N, 115°35.7'W and 22°52.7' N 109°50.98'W. Rare.



FIGURES 56–59. *Diacria*. **56a–c.** *Diacria trispinosa* (de Blainville, ex Lesueur MS, 1821), from website http://www.gastropods.com/6/Shell_1746.shtml; locality and shell height not mentioned (courtesy of Conquilogistas do Brasil). **57a–c.** *Diacria danae* van Leyen & van der Spoel, 1982; holotype, shell height 1.48 mm. From van der Spoel (1968: fig. 1A–C). **58a–b.** *Diacria danae* van Leyen & van der Spoel, 1982, composite photo, 2 shells, height 1.7 mm: off Makena, Maui, Hawaii; Nov. 29, 1991; from website <http://seaslugsofhawaii.com/species/Cavolinia-globulosa-a.html>; photographed at CAS (courtesy of Cory Pittman). **59a–c.** *Diacria schmidti* van Leyen & van der Spoel, 1982. Holotype NHMD-91521. Shell height c. 4.1 mm. From van der Spoel (1971: fig. 8A–C).

Suborder Pseudothecosomata Meisenheimer, 1905

Thecosomata de Blainville, 1824: 271 (pars).
 Pseudothecosomata Meisenheimer, 1905: 37.
 Peraclidacea Taylor & Sohl, 1962: 11.

Description. Anatomically different from Euthecosomata in structure of nervous system, digestive organs, and presence of proboscis.

Cymbolioidea Gray, 1840

Cymbuliidae [sic] Gray, 1840: 156.

Description. Shelled adult specimens only in Peraclidae, in other families only a minuscule shell during larval (veliger) stages, or with gelatinous pseudoconch.

Remarks. Three families (Peraclidae, Cymbuliidae, Desmopteridae) are members of this superfamily.

Peraclidae Tesch, 1913

Peraclididae Tesch, 1913: 71.

Procumbuliidae Tesch, 1913: 77.

Description. Shell sinistral with higher or lower spire, no umbilicus, but columella twisted, forming basal rostrum with membrane in most species; last whorl relatively large; subsutural crests and/or spines on apertural margin present in some species, epidermis with reticulate pattern (cuticulum). Epi- to mesopelagic, some species bathypelagic.

Peracle Forbes, 1844

? *Campylonaus* Benson, 1835a: 176 (*nomen nudum*, introduced with no species included). Type species *Atlanta reticulata* d'Orbigny, 1836 (SD Gray 1847: 149). Southern Atlantic or Indian oceans.

Peracle Forbes, 1844: 132, 186. Type species (M) *Peracle physoides* Forbes, 1844 = *Peracle reticulata* (d'Orbigny, 1836). Tropics and subtropics worldwide.

Peracis Pelseneer, 1888: 32 (unjustified emendation).

Procumbulia Meisenheimer, 1905: 13. Type species (M) *P. valdiviae* Meisenheimer, 1905. South Pacific Ocean, 34°14'S, 80°31'E.

Description. Same as for family.

***Peracle diversa* (Monterosato, 1875)**

(Figure 60)

Spirialis diversa Monterosato, 1875: 50. Syntypes MCZR (Gaglini & Villari 1994). Palermo, Sicily.

Peraclis apicifulva Meisenheimer, 1906: 122, pl. 5, fig. 9. Poorly preserved syntypes ZMB (van der Spoel 1976: 197). Four localities in Atlantic Ocean, 27°30'S to 21°N.

Peraclis brevispira Pelseneer, 1906: 146, pl. 12, figs 45, 46, 48, 49, 51. Syntypes lacking in NHMUK, only the label remains (van der Spoel 1976: 197). Gulf of Biscay.

Description. Shell width ~75% of total height, apical angle more than 90°; columellar membrane well-developed; subsutural crests present.

Distribution. In northeast Pacific to 30°N–50°N. Epi- to mesopelagic. Rare.

***Peracle reticulata* (d'Orbigny, 1835)**

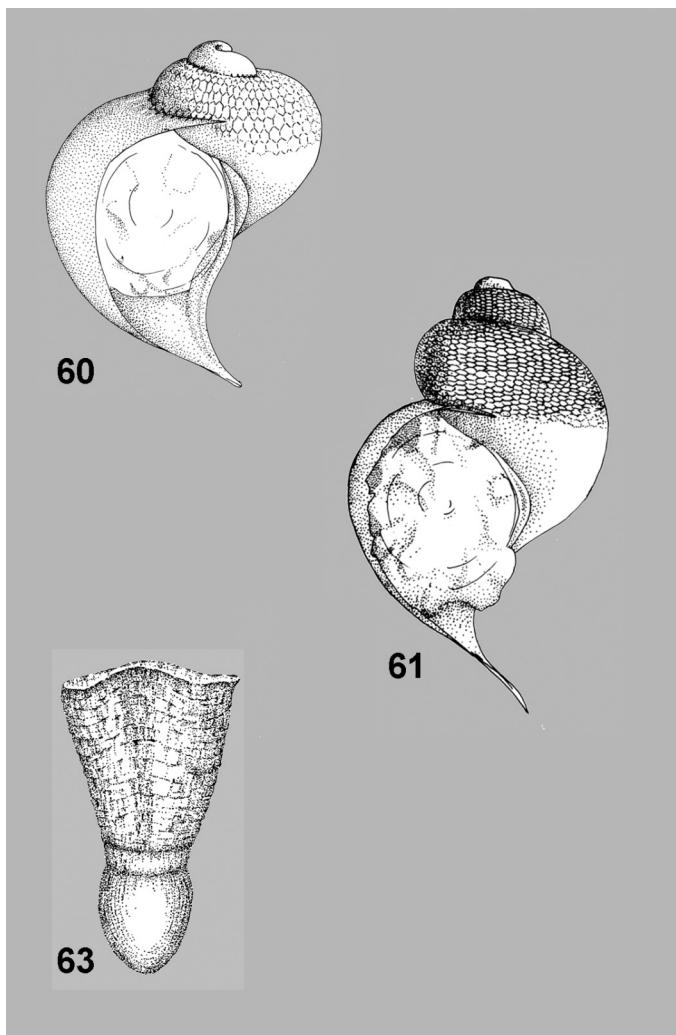
(Figure 61)

A[llanta] (sic) *reticulata* d'Orbigny, 1835: pl. 12, figs 32–35, 39;

Atlanta reticulata d'Orbigny, 1836: 178. Two fragmentary syntypes NHMUK 1854.12.4.39. Pacific Ocean 20°S, 89°W (of Paris).

Description. Shell about twice as high as wide, apical angle less than 90°; columellar membrane insignificant, no subsutural crests.

Distribution. Epipelagic, tropical and subtropical seas, worldwide. In northeast Pacific to c. 35°N. Uncommon.



FIGURES 60–63. *Peracle, Clione*. **60.** *Peracle diversa* (Monterosato, 1875). Atlantic Ocean, 16°06'N, 76°02'W; shell height c. 4 mm (from van der Spoel 1976, as *P. apicifulva*). **61.** *Peracle reticulata* (d'Orbigny, 1834), Atlantic Ocean, 07°22'N, 46°51'W; shell height c. 6 mm. (from van der Spoel 1976). **62.** *Clione limacina* (Phipps, 1774), adult specimen; Monterey Bay, California, body length 12 mm. Photo by Stephanie L. Bush. **63.** *Clione limacina* (Phipps, 1774), larval shell from plankton catch, Nova Scotia; shell height 0.36 mm (from Lalli & Conover 1973: fig. 7).

Suborder Gymnosomata de Blainville, 1824

Gymnosomata de Blainville, 1824: 273.

Remarks. Gymnosomata are pteropods without a shell in the adult stage. Larvae, however, have a minuscule calcareous (aragonitic) shell that is shed during metamorphosis. Although such larval shells were observed and described by Krohn (1860), it was the work of Lalli & Conover (1973) who succeeded in keeping gymnosomes under laboratory conditions, and observed them spawning. They described the larval shell of three identified species, including *Clione limacina* Phipps, 1774 (Figs 62–63 herein). Since then, various types of gymnosome larval shells have been recorded from sediment samples, but are usually unidentifiable to species. For an overview see Janssen (2012b: 451–455, pl. 26). As various other gymnosome species have been recorded from the northeastern Pacific (see van der Spoel 1976), larval shells may be collected in plankton tows or in sediment samples.

Several additional gymnosome pteropods occur in the northeast Pacific (van der Spoel 1976), but their larval shells are unknown: *Thliptodon diaphanus* (Meisenheimer, 1902), *Thliptodon* sp. nov., *Notobranchaea* cf. *macdonaldi* Pelseneer, 1886, *Pneumodermopsis* spp., and *Cliopsis krohni* Troschel, 1854.

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